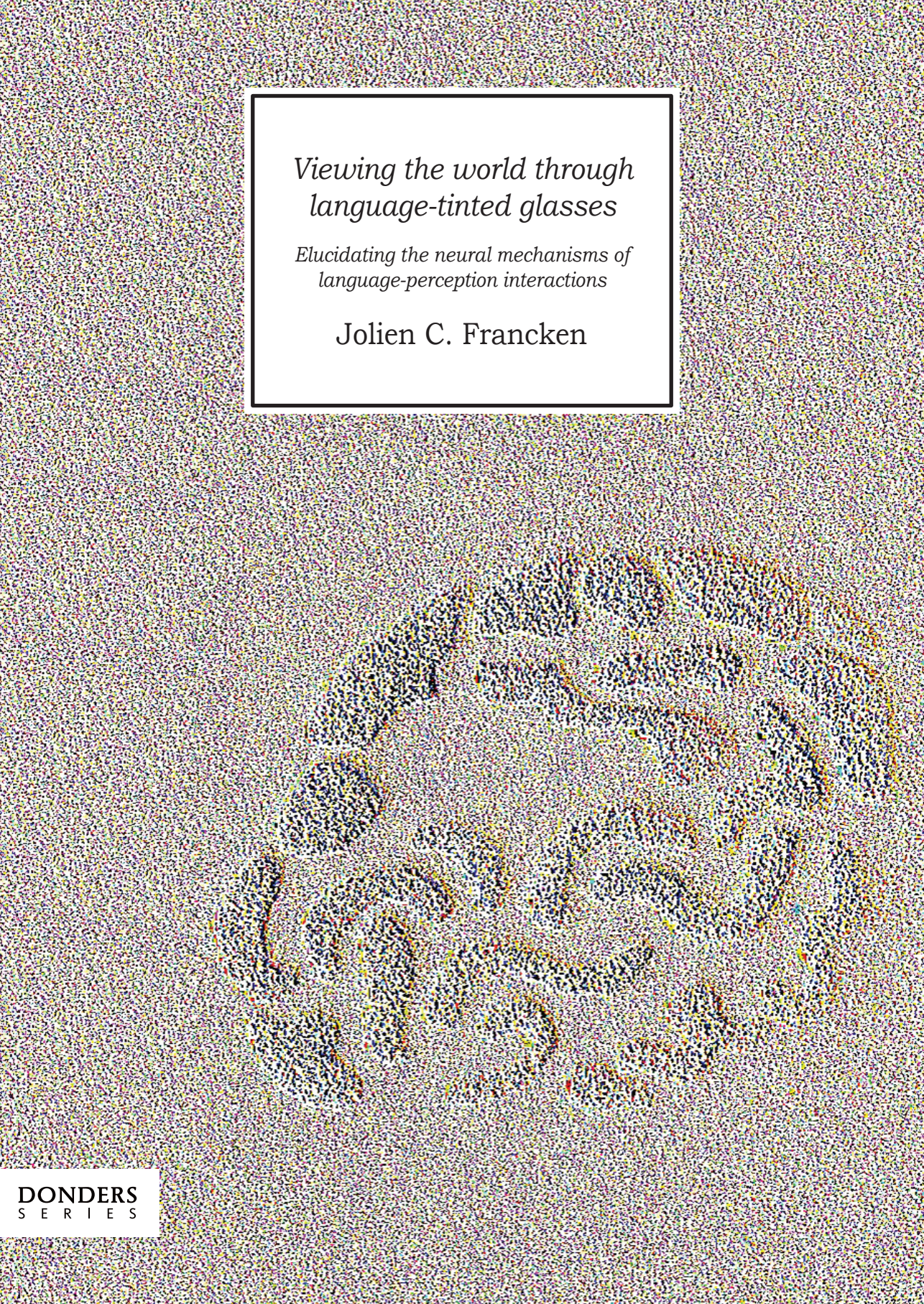
Viewing the world through language-tinted glasses

Elucidating the neural mechanisms of language-perception interactions

Jolien C. Francken



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VIEWING THE WORLD THROUGH LANGUAGE-TINTED GLASSES

ELUCIDATING THE NEURAL MECHANISMS OF LANGUAGE-PERCEPTION INTERACTIONS

Jolien C. FRANCKEN

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Jolien Cornélie FRANCKEN

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Promotor

Prof. dr. P. Hagoort

Copromotor

Dr. F.P. de Lange

Manuscriptcommissie

Prof. dr. A.S. Meyer
Prof. dr. A. Majid
Dr. S.-A. Rueschemeyer *University of York, Verenigd Koninkrijk*

De Eskimo's hebben wel duizend woorden voor sneeuw.

Een woord voor de sneeuwvlok die smelt in je oor,
dat dan jeuken gaat,
een woord voor het sneeuwen, de hele dag door,
in de stille straat.

Een woord voor de sneeuw langs een ruit in je klas
als het sneeuwen ging,
een woord voor de sneeuw op de kraag van de jas
van je lieveling.

De Eskimo's hebben wel duizend woorden voor sneeuw.

Een woord voor de sneeuwvlok die laag in de laan
op en neer beweegt,
een woord voor de zielige sneeuw, als de ijsbaan
wordt schoongeveegd.

Een woord voor de sneeuw die je huid openhaalt
Als de sneeuwjacht jaagt,
Een woord voor de sneeuw, in lantarens verdwaald,
die om aandacht vraagt.

De Eskimo's hebben wel duizend woorden voor sneeuw.

Een woord voor de sneeuw van de sneeuwman, die kijkt
of er niets aan schort,
terwijl toch iedereen duidelijk blijkt
dat hij kleiner wordt.

Een woord voor je moeder, een woord in een traan,
want wat wordt ze klein.
Tot ze net als de sneeuwman is overgegaan
in zonneschijn.

Uit: Het beloofde land, Willem Wilmink, 2002

CONTENTS

1

GENERAL INTRODUCTION

Jolien C. FRANCKEN

Every evening apparently before our eyes the sun goes down behind the stationary horizon, although we are well aware that the sun is fixed and the horizon moves (Von Helmholtz, 1925, p. 28)

1

1.1. INTRODUCTION

WHY do Eskimo's have more than hundred different words for snow? Many people have heard about this urban legend and might answer: Snow is a very important aspect of the Eskimo's environment, so they need an extensive vocabulary to be able to speak about all kinds of characteristics of snow that we do not care about. Mystery solved. Yet when you think about it, the answer provokes a much more puzzling question: If Eskimo's have a more extensive snow lexicon, does that mean that they do not only talk differently, but also see the world differently? In other words, do they have the capability to see more fine-grained distinctions because of their language?

Figure 1.1: Cartoon from Dave Coverly, 2009

In this thesis, I will provide empirical evidence suggesting that language affects how we perceive the world. I hope to convince the reader that perception is not a passive process intended to arrive at a veridical representation of the world, but instead an interpretative construction fundamentally influenced by language.

1.2. HISTORICAL AND EMPIRICAL BACKGROUND

1.2.1. HOW DO WE SEE THE WORLD? (PART I)

Before we had stopwatches to measure reaction times and fMRI scanners to look into brains, philosophers have long pondered to answer a central question: How do we see the world? In fact, they soon encountered an even more fundamental problem: Do we see what is really there? In other words, is the world we see around us the real world itself or merely an internal perceptual copy of that world generated by neural processes in our brain?

The former position refers to direct realism, the latter to indirect, or representative, realism. Representative realism states that the percepts that we experience, together with the further beliefs that we attain on the basis of them, form a representation of an independent realm of material objects in the (really existing) outside world (BonJour, 2001). Representative realism was adopted by Descartes and Locke, and is one of the

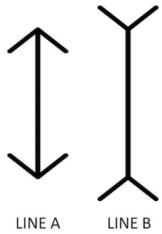


Figure 1.2: Müller-Lyer illusion. Line B appears longer than line A, although the actual physical lines have the same length.

key assumptions of cognitivism in psychology. Visual illusions, such as the Müller-Lyer illusion in Figure 1.2, provide support for representative realism. We perceive the right line (line B) as being longer, while we know that the actual physical lines have the same length. Thus, our percepts are different from what is out there in the world.

To come back to our initial question, how do we then 'construct' the world around us? Kant, and with him many other philosophers, argued that perception is inference, which means that our concepts, beliefs, and expectations influence what we see, or how we see something (Swoyer, 2003). For instance, in another famous visual illusion, the 'hollow face illusion', it is impossible to see a hollow face: As soon as a mask is viewed from the back, we immediately see the nose pointing out again (see Figure 1.3). This is explained by the role of expectations: Since we have never seen a hollow face in our lives, it is extremely unlikely that the current sensory information is correct. Therefore, it is quickly changed by our brain to produce the most plausible state of the world.

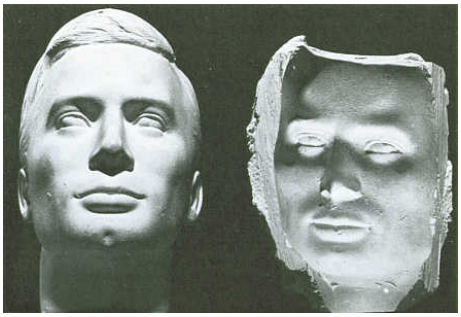


Figure 1.3: The hollow-face illusion. Bust (left) and mold (right) of a face. We perceive the face at the right as being convex, even though it is actually hollow. (Picture taken from brisray.com)

Cognitive psychology, neuroscience, and computational approaches attempt to explain the cognitive and neural processes of perceptual inference (see subsection 1.2.4). However, not only statistical regularities, such as the shape of a face, affect perception, but also cultural factors might influence how we see the world, a notion known as perceptual relativism (Swoyer, 2003). To illustrate how profound these cultural differences can be, let us take a look at the example of the Müller-Lyer illusion again. Segall and colleagues hypothesized that living in a 'carpentered world', such as a Western society surrounded

by a lot of rectangular shapes, straight lines, and square corners, would increase susceptibility to this illusion (Segall et al., 1966). Unless these rectangular objects are viewed from exactly the right angle, they will project a non-rectangular image onto the retina. Yet, we continue to perceive them as rectangular, which provides an explanation for the Müller-Lyer illusion. Indeed, when the researchers presented the Müller-Lyer stimuli to Zulu people, who live in round huts and plough their fields in circles rather than rows, it turned out that they were less susceptible to the illusion than people from the Western world.

1.2.2. A BRIEF HISTORY OF LINGUISTIC RELATIVITY

One of the most obvious cultural differences across the world is found in the variety of languages. In 1820, Von Humboldt was the first to explicitly link language and perception:

> The diversity of languages is not a diversity of signs and sounds but a diversity of views of the world (Trabant, 2000)

For him, and many others in the 19th and early 20th century, this observation implied that some languages were naturally superior to others and that the use of primitive languages left their speakers in intellectual poverty. 'Linguistic relativity' can be historically understood as a reaction to this widespread idea (Kay and Kempton, 1984). The research of Boas challenged Von Humboldt's view by showing that these languages were as systematic and as logically rich as any European language. According to Boas' student Sapir:

> When it comes to linguistic form, Plato walks with the Macedonian swineherd, Confucius with the head-hunting savage of Assam (Sapir, 1921, p. 219)

Sapir went a step further than Von Humboldt and proposed that because different languages represented reality differently, it followed that the speakers of different languages would perceive reality differently. Sapir's student Whorf, most famously associated with the linguistic relativity hypothesis, continued this line of thinking and moreover, was the first to actually make an attempt to study the effects of language on thought. He looked at Native American languages and tried to account for the ways in which differences in grammatical systems and language use affected the way their speakers perceived the world. Whorf's most important argument was his observation that the Hopi language had no concept of time:

> [Hopi contains] no words, grammatical forms, constructions or expressions that refer directly to what we call "time", or to past, present, or future (Whorf, 1956, p.57)

From this, he concluded that a Hopi had no general notion or intuition of time. However, Whorf has been criticized because most of his arguments were in the form of examples that were anecdotal in nature. In 1983, Malotki wrote a book called 'Hopi time' which starts with one of his 'Hopi field notes':

> pu' antsa pay qavongvaqw pay su'its talavay kuyvansat, pàasatham pu' pam piw maanat taatayna

> Then indeed, the following day, quite early in the morning at the hour when people pray to the sun, around that time then, he woke up the girl again (Malotki, 1983)

After Sapir and Whorf, linguistic relativity fell out of favor, unsurprisingly in the light of the almost complete lack of evidence to support the claims. The main theory from the 1960s until the 1980s was the 'universalist theory of language', formulated by Chomsky in the form of Universal Grammar, arguing that all languages share the same underlying, innate, structure. From this, he reasoned that learning a language does not affect universal cognitive processes such as thinking or perceiving. The work of Berlin and Kay focused on seeking universals in language and cognition. They showed that there are universal patterns in color perception across different languages, regardless of varieties in color terminology (Berlin and Kay, 1969). For instance, languages with only three color terms always have the focal colors black, white and red, which has been taken as strong evidence against linguistic relativity.

From the 1980s, with the rise of cognitive psychology and psycholinguistics, renewed interest in cultural differences resulted in new studies into the linguistic relativity hypothesis (Kay and Kempton, 1984; Lakoff, 1987; Levinson, 1996). For instance, Levinson reported that some Aboriginal groups who speak languages that rely on absolute spatial reference frames ("the garden stands north of the house") are very good at keeping track of where they are. Their language obliges them to have a compass in their mind to be able to speak properly, and indeed they maintain their orientation even in unfamiliar places or inside of buildings (Levinson, 1996). In the past two decades, researchers have continued to investigate cross-linguistic differences and their effects on cognition and perception. The linguistic relativity hypothesis formulated in the early 20th century has developed into a more nuanced version, with emphasis on the question to what extent language affects cognition. New studies have used implicit test measures and allowed for comparisons within-subjects (Masharov and Fischer, 2006)(see Section 1.3). Finally, the study of the effects of language on cognition is getting complementary support from cognitive (neuro)science.

1.2.3. HOW COGNITIVE SCIENCE BECAME EMBODIED

The early cognitive science model of the mind was very much inspired by the computer metaphor and influenced by predicate logic, propositional and computational formalisms (Meteyard et al., 2012). Here, internal cognitive symbols were thought to refer to external objects and events. The aim was to describe how these symbols are processed and how they are related, and not what their content is (e.g., Fodor, 1975; Jackendoff, 2002). Yet, a problem for this model was to explain how these symbolic representations refer to the outside world.

In the 1990s, opponents of the symbolic view of cognition argued that from describing the internal manipulations of symbols, meaning could not be established. They came up with a different approach: 'Embodied cognition'. Here, cognitive functions, such as thinking and speaking, are about real-world action rather than symbolic representation. For instance, when we hear the word "dog", embodied semantics states that we reconstruct the associated sensory and motor information that we experience during an actual encounter with a dog. Thus, the distinction between non-linguistic and linguistic forms

of representation disappears. To result in stable representations, embodied cognition accepts that the environment has to be internalized, but rather than by transducing sensory input or motor output, the signal is recreated or 'simulated'. Thus, the content of a representation has the same form as actual sensory and motor information.

An influential finding provided evidence for embodied cognition: The discovery of 'mirror neurons' (di Pellegrino et al., 1992). Di Pellegrino and colleagues observed that neurons in the ventral premotor cortex of the macaque monkey not only responded to actual movements, but also to the observation of another monkey performing the same movements. Inspired by these findings, it was proposed that semantic representations are also embodied, meaning that simulation of sensori-motor information is constitutive of language comprehension (Barsalou et al., 2003; Gallese and Lakoff, 2005; Glenberg and Kaschak, 2003). Researchers provided evidence for embodied semantics by showing that 1) the same brain areas and processes are involved in performing an action and reading about the action (e.g., Hauk et al., 2004); 2) seeing a particular event and reading about the same event results in behavioral facilitation or interference (e.g., Stanfield and Zwaan, 2001); 3) these sensori-motor effects occur simultaneously with or before semantic processing (Hauk et al., 2008).

Since then, the debate has focused on what counts as evidence for the 'same' brain areas and processes. For instance, does the fact that the motor cortex is somatotopically activated by reading face, hand and foot words prove that during language comprehension the respective actions are simulated in the motor cortex? An alternative explanation would be that the words are semantically processed in amodal conceptual or association areas and as a consequence activation could spread to the motor cortex (Mahon and Caramazza, 2008). Thus, during the past ten years, the discussion has been about necessary and sufficient conditions for understanding language (Weiskopf, 2010; Willems and Casasanto, 2011). Meteyard and Vigliocco distinguish four positions along a continuum, ranging from truly symbolic theories, to theories proposing only a secondary role for sensori-motor areas in semantics, to embodied semantics, postulating that sensori-motor simulation is necessary and sufficient for language comprehension (Meteyard et al., 2012).

Ultimately, the debate comes down to the question: What does understanding language actually mean? Are there any 'core' components of comprehension? And is my understanding of the word "ballet" the same as the understanding of the word by a professional ballet dancer? Regardless of the answers to these conceptual, rather than empirical, questions, for the current discussion it is important that the pursuit of confirming the embodied semantics theory has resulted in the design of experiments targeting the effects of language on perception and perceptual processing.

1.2.4. HOW DO WE SEE THE WORLD? (PART II)

In subsection 1.2.3 I showed that the theory of embodied cognition was formulated as a direct reaction to symbolic, amodal theories of cognitive science. In the field of perception, a similar reaction has resulted in the proposal that perception is not an encapsulated, passive feed-forward process of representing the outside world, but rather a process of inference resulting from recurrent interactions between bottom-up input and top-down factors (Gilbert and Li, 2013; Gregory, 1980; Summerfield and de Lange, 2014; Von Helmholtz, 1925). Perception is here understood as a decision-making process, in

which potentially ambiguous information from the local environment has to be resolved into a coherent percept. Prior information about what is probable in the sensory environment may help the brain decide among competing options and thereby influences how we see the world (Summerfield and Egner, 2009). These priors might be formed because some stimuli are more frequent, often co-occur with other stimuli, or because they are stable over time (Summerfield and de Lange, 2014). For instance, when you hear a barking sound, you might expect to see a dog (multisensory conditional probability), and not a wolf (statistical learning). Moreover, if you happen to be a dog-owner and you are in your own house, it is very unlikely that your dog has changed appearance since you saw it last time: It is probably still of the same size, color, and shape (temporal autocorrelation).

Recently, researchers started to investigate the neural and cognitive mechanisms of the interactions between prior information and sensory input. For instance, they asked where priors are represented in the brain. Summerfield et al. (2006) used an elegant paradigm in which participants had to view alternating pictures of degraded faces, houses and cars. In each block of trials, they had to use a different task. In face blocks, they judged whether each object was a face or not, while on house blocks they had to detect houses. In this way, the stimulus characteristics were completely identical and only the top-down strategy of the participants differed. They found that the medial frontal cortex responded to the face blocks, and that there was an increase in top-down connectivity from the frontal cortex to face-selective visual areas, potentially inducing the formation of a specific stimulus template.

Thus, in this study participants were biased to process one type of information over another. However, the prior probability of the occurrence of information (likelihood) was not manipulated: Face stimuli were equally frequent as the other stimuli. Therefore, it has been argued that these findings might reflect attention or relevance instead of prior expectation (Rahnev et al., 2011). Later studies attempted to disentangle these two often-conflated concepts and demonstrated that they have opposite effects on early visual neural activation (Kok et al., 2012b). While attention boosts activation in early visual cortex, expectation decreases activation. This expectation-effect is explained by the predictive coding theory (Friston, 2005). According to this theory, higher-order regions send predictions to lower-order regions, and these predictions are then compared to the sensory evidence. When they match, a small prediction error results and this induces a relative decrease in neural activation, whereas when there is a mismatch, a large prediction error leads to increased activation (Summerfield et al., 2008). Kok and colleagues refined this hypothesis by showing that the reduction in overall neural activation after valid expectations is accompanied by an increase in information representation, i.e., expectations sharpen predicted representations by suppressing inconsistent bottom-up signals (Kok et al., 2012a).

In addition to expectations, other top-down factors influence how we see the world around us as well. Attention and task-set also have been shown to interact with early visual processing and affect our percepts (Gilbert and Li, 2013). In line with this view, linguistic information may also provide contextual feedback to perceptual systems, since the associations between words and the external objects and events to which they refer have been created and strengthened from our early childhood. Therefore, although language only has an arbitrary relationship with the physical world through cultural

learning, it might act as a prior on perception.

1.2.5. CONCLUSION

With this historical and empirical background I intended to show how the current empirical research into the effects of language on perception has evolved from three different fields. First, linguists are interested to see how cross-cultural differences in language affect cognition and perception. Second, psycholinguists and cognitive neuroscientists studying the nature and organization of the semantic system look at perceptual processing to support their embodied semantics hypothesis. Finally, cognitive neuroscientists from the field of (visual) perception attempt to show how top-down factors, including language, influence what we perceive.

1.3. STUDYING THE EFFECTS OF LANGUAGE ON PERCEPTION

DOES the fact that we acquired linguistic knowledge over our lifetime matter for how we perceive the world? As I discussed in section 1.2, many believe this must be the case. The historical and empirical background showed that there are three complementary strands of research from which studies into the effects of language on perception have naturally evolved. Yet, still not many studies have been performed to directly investigate the phenomenon. Recently, two main approaches have been used to study language-perception interactions.

1.3.1. EXPERIMENTAL APPROACHES

First, emerging from the field of linguistics, cross-linguistic studies compared groups of people with different native languages to see how this affects their cognitive functions. A classic example is the color perception domain. The physics of color perception provide us with a continuous color spectrum, while in our language we use more or less discrete categorical distinctions to describe colors: Blue is different from green. Winawer et al. (2007) used this incongruity to test whether the fact that English and Russian color terms divide the color spectrum differently would result in differences in color perception. The rationale behind this is the fact that the presence of a categorical border between two colors might improve discrimination, since this border enhances the subjective appearance of color difference. Unlike English, the Russian language makes an obligatory distinction between lighter blues ("goluboy") and darker blues ("siniy"). In the experiment, English and Russian speakers discriminated blue stimuli that spanned the siniy and goluboy border. Russian speakers were faster to discriminate two colors when they fell into different linguistic categories in Russian (between-category) than when they were from the same linguistic category (shared the same name; within-category). The effects were stronger for difficult discriminations (i.e., when the colors were perceptually close) than for easy discriminations. English speakers tested on identical stimuli did not show a category advantage in any of the conditions, showing that people speaking different languages perceive colors in different ways.

Second, researchers from the field of cognitive (neuro)science studied language-perception interactions by creating different experimental conditions within a group of participants from the same language community. The main question here is whether and

how linguistic knowledge affects visual perception. These experimental approaches are inspired by the embodied cognition theory and prediction accounts of perception.

Several behavioral studies have investigated the interaction between linguistic information and visual perception in behavioral experiments, demonstrating that task-irrelevant or even implicit language nevertheless affects perception of shape, objects, directional perspective, motion direction, color, and contrast sensitivity (Lupyan and Spivey, 2010a; Meteyard et al., 2007; Pelekanos and Moutoussis, 2011; Richardson et al., 2003; Stanfield and Zwaan, 2001; Zwaan et al., 2002). For instance, Meteyard and colleagues showed that task-irrelevant motion words affected visual motion detection (Meteyard et al., 2007). When motion words described movement that was congruent with visual motion direction, detection sensitivity was increased and participants more often reported that they perceived coherent movement in the cued direction. Not only the semantic content of linguistic information, but also phonological and syntactic aspects have been shown to affect what we see (Boroditsky et al., 2003; Meyer et al., 2007). Taken together, these studies provide converging evidence for the idea that language affects perception.

More recently, studies using neuroimaging methods investigated the neural mechanisms of language-perception interactions. One approach focused on the effects of linguistic material on perceptual processing, without taking into account the cognitive and behavioral consequences of these effects. For instance, participants were presented with written action verbs or motion words. The empirical findings happened to be equivocal: Some fMRI studies reported that language affects early stages of visual processing (Revill et al., 2008; Rueschemeyer et al., 2010; Saygin et al., 2010) while others dispute this and observed effects in areas more downstream in the ventral visual cortex (Bedny et al., 2008; Dravida et al., 2013; Wallentin et al., 2011).

A second approach is to present visual stimuli in isolation and test whether pre-existing linguistic knowledge affects perceptual decision-making (e.g., discrimination, detection or categorization). This approach is used in the color perception domain, for example in the study of Winawer et al. (2007) that I discussed above. Many of these studies showed that there is 'categorical perception' for color: Faster or more accurate visual discrimination of stimuli that cross a linguistic category boundary (e.g., a blue and a green colored square compared to two shades of blue). Neuroimaging studies using electrophysiology or fMRI aimed to test whether this categorical perception effect arises from early sensory processing or from later processing stages. The results are mixed: Some found early effects (Fonteneau and Davidoff, 2007; Thierry et al., 2009), some later effects (semantic processing stages)(Tan et al., 2008), and some reported both (Holmes et al., 2009; Ting Siok et al., 2009).

A third possibility to investigate the locus of language-perception interactions is to present both linguistic material and visual stimuli, similar to the previously described behavioral experiments, and to see where and how the brain integrates the two sources of information. So far, only a few studies have used this latter strategy (Hirschfeld et al., 2011; Landau et al., 2010; Sadaghiani et al., 2009). A good example is an EEG study by Landau et al. (2010) who studied the temporal dynamics of the effects of linguistic primes on face perception. They focused on the N170, a reliable evoked response elicited after the visual presentation of faces, and in addition they assessed the consequences of the

linguistic primes for performance in a separate behavioral experiment. The primes were auditory presented sentences that described either faces or places (e.g., "The farmer has freckles on his cheeks"), followed by an interval of 500 ms and next the presentation of a picture of either a face or a place. The N170 was larger for face pictures that followed face-related sentences compared to face pictures that followed place-related sentences over the posterior part of the left hemisphere. The authors argued that the early timing as well as the posterior locus of the effects provides evidence for the hypothesis that the linguistic primes modulate early visual processing, rather than later stages of perception.

In sum, the effects of language on perception have been studied cross-culturally and with within-subjects approaches, using behavioral measures and neuroimaging methods. The latter strategy includes studies presenting either linguistic material and looking at its neural consequences, or presenting only visual stimuli and inferring the effects of existing lexical knowledge, or looking at the interaction between linguistic and visual material. Regardless of the approach, evidence appears to be mixed: Some observed effects at an early visual processing stage, while others reported later effects at semantic or decision stages.

1.3.2. LATERALIZATION TO THE LEFT HEMISPHERE?

In a cleverly designed behavioral study, Gilbert and colleagues tested the possibility that language affects perception more strongly in the left than in the right hemisphere, providing evidence for the language-specificity of the behavioral language-perception interactions that had been reported until then (Gilbert et al., 2006). The rationale behind their design is that (given the contra-lateral nature of visual projections to the cortex) visual color stimuli presented in the right visual field (RVF) relative to the left visual field (LVF) would be more susceptible to modulation by the left-lateralized language system. In their study, English-speaking participants performed a visual search task in which they had to indicate which of twelve color patches, centered around a fixation cross, had a different color than the rest (see Figure 1.4).

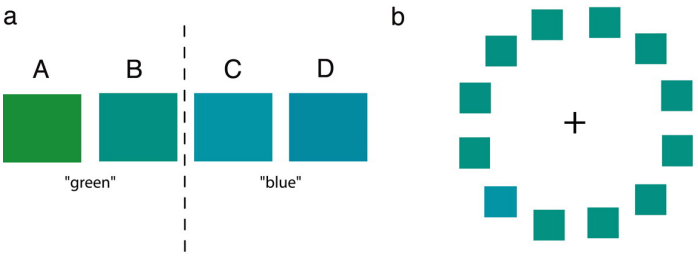


Figure 1.4: The experimental design of Gilbert et al. (2006). A. Four different color patches were used. B. Sample display for the visual search task. In this example, the target color is presented at the left side of the screen.

The odd color could be present at the left or the right side of the screen. Crucially, the target and distracter patches belonged to either the same color category, e.g., a light green patch surrounded by dark green patches (within-category conditions, e.g., A vs. B), or to different categories, e.g., a light green patch surrounded by light blue patches (between-category conditions, e.g., B vs. C). Similar to the study of Winawer

et al. (2007), the four color patches had equidistant hues. The results showed that the linguistic category boundary between the light green and light blue hues (B vs. C) affected color discrimination: Participants were faster for between-category conditions relative to within-category conditions. However, this effect was only present when the target patch was presented in the RVF. Interestingly, in a follow-up experiment with the same design but with an additional verbal interference task (remembering a list of eight digits), the effect was abolished, while an interfering visual task (remembering a random dot pattern) had no such effect. In a later study by Gilbert and colleagues they extended their findings from color patches to the discrimination of silhouettes of dogs and cats, confirming that perception was affected by linguistic categories in the RVF only (Gilbert et al., 2006).

A couple of neuroimaging studies have subsequently studied the lateralization of categorical color perception more directly (Fonteneau and Davidoff, 2007; Holmes et al., 2009; Kwok et al., 2011; Liu et al., 2009, 2010; Mo et al., 2011; Ting Siok et al., 2009). In an fMRI study, Ting Siok et al. (2009) found that discriminating between-category colors (versus within-category) elicited faster and stronger response in the left hemisphere language regions, especially when the colors were presented in the RVF. They further found that only for between-category stimuli activation was significantly enhanced in the visual areas responsible for color perception.

Taken together, these studies suggest that language exerts stronger or exclusive effects for stimuli presented in the RVF. However, recently others have failed to replicate these lateralized categorical color effects (Brown et al., 2011; Liu et al., 2009; Ting Siok et al., 2009; Witzel and Gegenfurtner, 2011). Witzel and Gegenfurtner performed ten different versions of the two original experiments of Gilbert et al. (2006) and Drivonikou et al. (2007) with overall 230 participants (Witzel and Gegenfurtner, 2011). They emphasized that they carefully controlled the rendering of the stimulus colors and determined the genuine color categories with an appropriate naming method, in contrast to previous studies. They obtained the classical categorical color perception effect, however, these effects were not lateralized, but appeared in both visual fields. Thus, although the idea that language affects perception more strongly in the left relative to the right hemisphere seems intuitive, the empirical evidence remains inconclusive.

1.4. AIM OF THIS THESIS

MANY empirical studies have investigated whether, where and how language affects visual perception using different approaches and methodologies. Currently, there exists a general consensus that language can indeed affect perception, however the results with respect to the cognitive and neural mechanisms underlying the phenomenon are still largely unclear. In this thesis, I will directly target the question of how language affects perception.

1.4.1. LEVEL AND MECHANISM

I aim to investigate at which level language affects perception and what are the cognitive and neural mechanisms underlying these interactions. There are several candidate mechanisms, each of which will be discussed below.

EARLY VISUAL PROCESSING STAGE: EMBODIED SIMULATION

In subsection 1.2.3 I explained how the theory of embodied cognition could account for language-perception interactions. Embodied theories of semantics predict that the comprehension of words or sentences referring to a particular perceptual event should influence perceptual processing of that event, since comprehension and perception recruit the same (cognitive and neural) system. Support for the idea that language comprehension involves embodied simulation first came from neuroimaging studies showing that processing language referring to motor actions, such as "kick" and "walk", activates premotor regions used for those actions (Aziz-Zadeh and Damasio, 2008; Aziz-Zadeh et al., 2006; Hauk et al., 2004; Tettamanti et al., 2005). A couple of behavioral and fMRI studies have applied the same logic to the domain of motion language (Meteyard et al., 2007; Saygin et al., 2010). For example, words referring to motion, such as "rise" and "fall", are thought to recruit sensory systems involved in perceiving motion. However, evidence for involvement of the primary visual motion-selective cortex in motion language comprehension is debated.

EARLY VISUAL PROCESSING STAGE: PREDICTION

According to predictive theories of cognitive and neural processing, the brain uses all available prior information to support perceptual inference (Summerfield and de Lange, 2014)(see subsection 1.2.4). Language may be one of many sources of information that could be used to predict what is coming up next in the (visual) environment. Following this line of reasoning, predictions derived from language comprehension could affect low-level visual processing as a consequence (Lupyan, 2012a). This idea is consistent with studies demonstrating the selective effect of non-linguistic expectations on (early) visual areas (Kok et al., 2012a; Summerfield and de Lange, 2014; Summerfield et al., 2008).

EARLY VISUAL PROCESSING STAGE: VISUAL IMAGERY

Language might affect perception indirectly, by means of visual 'mental imagery', which is the conscious, internal generation of images (Kosslyn et al., 2001). This process would require feedback from regions higher up in the cortical hierarchy in order to affect low-level sensory processing. In line with this hypothesis, participants showed a motion aftereffect illusion when reading stories describing motion events, which can be interpreted as evidence for direction-selective motion adaptation in the visual system (Dils and Boroditsky, 2010). Interestingly, individuals differed in how early in the story the effect appeared, and this difference was predicted by the strength of an individual's motion aftereffect following explicit motion imagery. Thus, when imagery is sufficiently vivid, language appears to induce changes in the visual system. Given that in many language-perception experiments the linguistic material precedes the visual stimuli, the enduring effects of these mental images could lead to modulatory effects on processing and perception of subsequent visual stimuli. According to the theory of embodied semantics, mental imagery might even be a component of language understanding in general (Saygin et al., 2010).

POST-SENSORY PROCESSING STAGE: CONCEPTUAL INTERACTION

Instead of occurring at an early stage in visual cortical regions, the interaction between language and perception might occur at a later, conceptual stage in language-processing

regions of the brain. Masharov and Fisher proposed that the categorical color perception effects might arise as a result of automatic activation of color names in the language system (Masharov and Fischer, 2006). Tan et al. (2008) and Ting Siok et al. (2009) have provided fMRI evidence for this hypothesis showing that language regions in the brain are automatically activated even though color naming is not required to perform a color discrimination task. Klemfuss et al. (2012) also suggested a conceptual level interaction as an explanation for the lateralized categorical color perception effects from Gilbert et al. (2006). Color names (in the left hemisphere) might be retrieved more easily or quickly for RVF compared to LVF stimuli and therefore exert a stronger influence on task performance. Thus, according to the conceptual level mechanism, visual information is processed up to a conceptual level, and it is here at the conceptual level that language-perception interactions take place.

POST-SENSORY PROCESSING STAGE: DECISION AND MEMORY PROCESSES

The Stroop effect is a classic example of priming at the decision or response selection level (MacLeod, 1991). Since the task requires a response to the stimulus color, the (irrelevant) lexical codes of word names also automatically activate a response, resulting in interference. The study of Meteyard et al. (2007) could also be interpreted as providing evidence for an interaction at later decision stage of perceptual decision-making. Motion words could have primed perceptual decisions about motion direction at a higher-order decision level, rather than activating representations in early visual cortex, as predicted by embodied simulation, mental imagery, or prediction accounts. Along similar lines, language might affect perception by interacting with working memory processes that are involved in perceptual tasks (Klemfuss et al., 2012; Mitterer et al., 2009).

1.4.2. LATERALIZATION OF EFFECTS

A second aim of this thesis is to investigate the potential laterality of language-perception interactions. Previous studies have shown that effects of language on perception are stronger in the RVF compared to the LVF, however these findings are debated. Furthermore, most of the studies have focused on color perception and it is therefore currently unclear whether these effects extend to other domains.

1.4.3. EXPERIMENTAL APPROACH

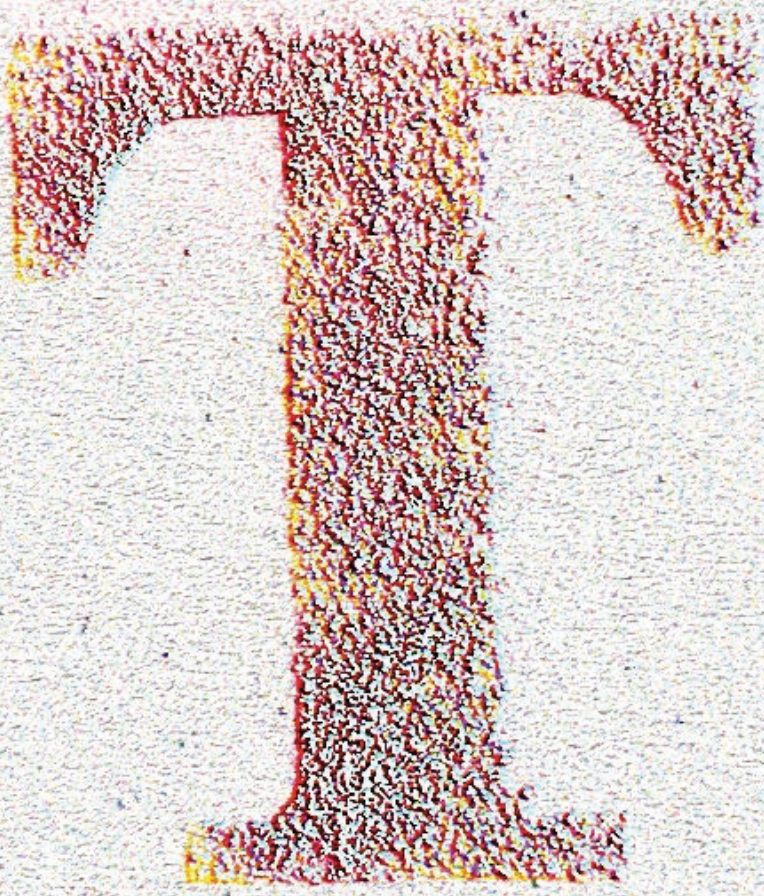
How will I study the level and mechanism of language-perception interactions and the potential lateralization of the effects? First, I will focus on semantic effects of language on perception, rather than phonological, morphological or syntactic effects (see for example Boroditsky et al., 2003; Boutonnet et al., 2012; Meyer et al., 2007). Therefore, in the remainder the terms "language" and "concepts" will be used interchangeably. Second, I will study effects of language on perception, and not the other way around (e.g., Kaschak et al., 2005; Meteyard et al., 2008; Rueschemeyer et al., 2010). I will make experimental comparisons within subjects speaking the same native language, instead of using a between-subjects approach and a focus on cross-linguistic differences. I will test healthy, adult participants and use the concepts that they already have acquired at an early age, thus not focusing on language acquisition in developing children or the learning of new concepts (e.g., Athanasopoulos et al., 2010). Finally, I will use a combination of

behavioral and neuroimaging methods to study online interactions of linguistic and visual stimuli. This contrasts with approaches in which only linguistic stimuli (e.g., action verbs), or on the other hand, only visual stimuli (e.g., colored squares) are used.

In the first three empirical chapters, I use visual random-dot motion paradigms in combination with single-word primes that are related or unrelated to motion. To study the dependence of the effects of language on perception on different factors, I manipulate the visual field in which the visual stimuli are presented, as well as awareness of and attention to the (motion) words. In the fourth chapter, I additionally study the effects of concept hierarchy and typicality on the effects of language on the visual perception of objects. Finally, I use different types of experimental tasks, ranging from detection, to discrimination and categorization of visual stimuli.

1.4.4. OVERVIEW OF CONTENT

I will address the question on the mechanism of language-perception interactions in four empirical chapters. In Chapter 2, which includes a behavioral and an fMRI study, we investigate the effects of motion words on the perception of visual motion that are presented either in the LVF or RVF. In Chapter 3, we distinguish between a feed-forward and a feedback model of language-perception interactions. In a behavioral experiment with a similar design as Chapter 2, we use backward masked motion words and test whether these still affect motion perception to disentangle the two models. Chapter 4 investigates the effects of awareness and attention on the neural locus of the effect of motion language on motion perception. In the behavioral and fMRI experiments described in Chapter 5, we use a semantic categorization task on pictures of animals and tool in combination with word cues. To study the potential different effects of cues at different levels of the conceptual hierarchy, we create category cue and exemplar cue conditions. Following these empirical chapters, Chapter 6 is an opinion article about the study of embodied semantics.



2

THE BEHAVIORAL AND NEURAL EFFECTS OF LANGUAGE ON MOTION PERCEPTION

Jolien C. FRANCKEN, Peter KOK, Peter HAGOORT and Floris P. DE LANGE

Perception does not function as an isolated module but is tightly linked with other cognitive functions. Several studies have demonstrated an influence of language on motion perception, but it remains debated at which level of processing this modulation takes place. Some studies argue for an interaction in perceptual areas, but it is also possible that the interaction is mediated by 'language areas' that integrate linguistic and visual information. Here, we investigated whether language–perception interactions were specific to the language-dominant left hemisphere by comparing the effects of language on visual material presented in the right (RVF) and left visual fields (LVF). Furthermore, we determined the neural locus of the interaction using fMRI. Participants performed a visual motion detection task. On each trial, the visual motion stimulus was presented in either the LVF or in the RVF, preceded by a centrally presented word (e.g., "rise"). The word could be congruent, incongruent, or neutral with regard to the direction of the visual motion stimulus that was presented subsequently. Participants were faster and more accurate when the direction implied by the motion word was congruent with the direction of the visual motion stimulus. Interestingly, the speed benefit was present only for motion stimuli that were presented in the RVF. We observed a neural counterpart of the behavioral facilitation effects in the left middle temporal gyrus, an area involved in semantic processing of verbal material. Together, our results suggest that semantic information about motion retrieved in language regions may automatically modulate perceptual decisions about motion.

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2.1. INTRODUCTION

PERCEPTION is influenced by a host of top-down factors, such as attention, expectation, and task set (Gilbert and Li, 2013). It has been hotly debated whether language also influences perception. Recent studies observed an influence of language on the perception of color (Gilbert et al., 2006; Regier and Kay, 2009; Thierry et al., 2009), faces (Anderson et al., 2011; Aziz-Zadeh et al., 2008; Landau et al., 2010), objects (Hirschfeld et al., 2011; Lupyan and Ward, 2013; Stanfield and Zwaan, 2001), and motion (Dils and Boroditsky, 2010; Meteyard et al., 2007; Pavan et al., 2013). Although evidence for an interaction between language and perception has been forthcoming, it remains unclear at which level of processing this interaction takes place.

Some studies have suggested that language interacts with perception by modulating sensory processing, by showing that language leads to changes in speed and sensitivity of perceptual decisions (Barsalou, 2008; Lupyan and Spivey, 2010a; Meteyard et al., 2007), and that language modulates neural activity in sensory cortex at an early stage during a perceptual task (Hirschfeld et al., 2011; Mo et al., 2011; Thierry et al., 2009). Alternatively, language-perception interactions could take place in 'language areas', by biasing the perceptual decision at the semantic level (Tan et al., 2008). Lexical semantic selection is mediated by the middle temporal gyrus of the left hemisphere (Indefrey and Levelt, 2004, 2000), and this region has been shown to integrate semantic information from different modalities (Beauchamp et al., 2004; Noppeney et al., 2008; Schneider et al., 2008). Therefore, it is conceivable that lexical semantic processes may bias the translation of sensory evidence into perceptual decisions.

One factor that may influence whether language modulates perception is the hemisphere that is processing the sensory information. Several studies found a stronger effect of language on perception when visual stimuli are presented in the right visual field (Drivonikou et al., 2007; Gilbert et al., 2006, 2008; Mo et al., 2011; Zhou et al., 2010). Since both right visual field stimuli and lexical items are processed by the left hemisphere, these findings are in line with an interplay between perceptual and language processes, but they do not elucidate the processing stage at which this interaction occurs.

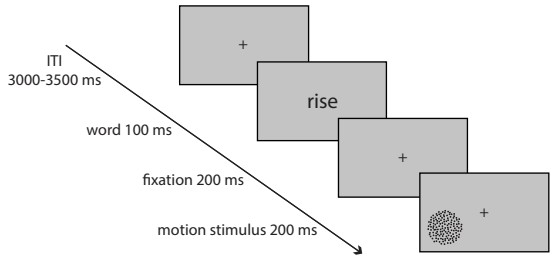

Figure 2.1: Task design. A congruent, incongruent, or neutral word is displayed before every motion detection trial. The visual motion stimulus is presented either in the left or right lower visual field. The dots move upward or randomly for half of the participants and downward or randomly for the other half. ITI = intertrial interval.

In the current study, we aimed to characterize the behavioral effects of motion language on motion perception, and to determine the neural locus of these effects. To this

end, we measured behavioral performance and neural activity using fMRI while participants were engaged in a motion detection task. We presented subjects with a visual motion stimulus in either the left or in the right visual field. The motion stimulus was preceded by a motion word (e.g., "rise"), which was briefly flashed at the center of the visual field. The word had no predictive relation with the direction of the visual motion stimulus, and subjects were told that they could ignore the word. Importantly, the motion word could be congruent, incongruent or neutral with respect to the subsequent visual motion stimulus. This allowed us to probe whether and where semantic linguistic stimuli influence motion perception, as a function of the hemisphere that processes the sensory information.

2.2. MATERIALS AND METHODS

2.2.1. PARTICIPANTS

The experiment consisted of a behavioral and a neuroimaging (fMRI) part. Twenty-two participants (5 males, 17 females; age range: 18-31 years) were included in the behavioral study and twenty-five (6 males, 19 females; age range: 18-28 years) participants engaged in the fMRI study. All participants were right-handed, had normal or corrected-to-normal vision, were native Dutch speakers and had no reading problems. Compensation was 8 euros for participation in the behavioral study and 25 euro for participation in the fMRI study. The study was approved by the regional ethics committee, and a written informed consent was obtained from the subjects according to the Declaration of Helsinki. Three participants were excluded from the fMRI study. One participant had excessive head movement during scanning (>5 mm), and two subjects could not maintain vigilance during the experiment.

2.2.2. STIMULI

Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997) within MATLAB (MathWorks, Natick, MA, US), and displayed on a Samsung SyncMaster 940BF monitor (refresh rate: 60 Hz, resolution: 1280x1024) in the behavioral experiment and on a rear-projection screen using an EIKI projector (refresh rate: 60 Hz, resolution: 1024 × 768) in the fMRI experiment. To ensure constant viewing position and angle in the behavioral experiment, we used a chin and forehead rest to restrain head position. Both words and visual motion stimuli were presented in white (220 cd/m2 behavioral experiment; 126 cd/m2 fMRI experiment) on a light-gray background (38 cd/m2 behavioral experiment; 33 cd/m2 fMRI experiment). Twenty-five verbs describing each direction of motion (upward and downward) and twenty-five neutral verbs (matched for lexical frequency (taken from the CELEX database), number of letters, number of syllables, and concreteness (all p>0.10) were used in the experiment (see Table 2.1).

The visual random-dot motion (RDM) stimuli consisted of white dots (density: 2.4 dots/deg; speed: 14.0 deg/s) that were plotted within a circular aperture (radius: 11.0 deg) that was presented in either the lower left or lower right quadrant of the screen. During random motion trials, all dots were replotted in a random location every monitor refresh, leading to no coherent movement on the screen. During trials with coherent motion, a certain percentage (see below) of the dots was chosen on every frame to be replotted in

the coherent direction on the next frame.

The percentage of the dots moving coherently in one direction (upward for half of the subjects, downward for the other half, see below) was estimated for each subject using a Bayesian adaptive staircase procedure (Watson and Pelli, 1983). The staircase procedure was done jointly for LVF and RVF stimuli. This was done to yield comparable task difficulty and performance for all subjects. During the training phase, subjects first practiced the motion detection task in three blocks with fixed coherence levels (0.8, 0.4, and 0.2 respectively). The coherence levels of the two subsequent training blocks were adjusted on the basis of performance in the previous block. The coherence level after the fifth training block was taken as the starting point for the adaptive staircase procedure in the threshold estimation block. Threshold for detection was defined as the percentage of coherent motion for which the staircase procedure predicted 75% accuracy. The coherence level was fixed during each block of trials, but was updated after each block with the same Bayesian staircase procedure to accommodate potential practice and fatigue effects over the course of the experiment.

2.2.3. PROCEDURE

Direction of motion was counterbalanced across subjects, i.e., half of the subjects were presented with upward and the other half with downward motion stimuli. A central fixation cross (width: 0.3 degrees) was presented throughout the trial, except when a word was presented. Each trial started with a centrally presented word (duration: 100 ms), which could either be a motion word or a neutral word, and which was followed by a 200 ms inter-stimulus interval (see Figure 2.1).

Presentation of the words was fully randomized within each block of the experiment. We instructed subjects to ignore the word and maintain fixation. Next, a visual RDM stimulus was presented (duration: 200 ms) in either the left visual field (LVF) or in the right visual field (RVF). Subjects had to indicate as quickly and accurately as possible whether the RDM contained coherent motion, while fixating at the central fixation cross. The brief presentation time of the RDM stimulus (200 ms) served to minimize the chance of eye movements to the stimulus, as saccade latencies are in the order of 200 ms (Carpenter, 1988).

Subjects were instructed to respond as quickly and accurately as possible by pressing a button with either the left or right index finger in the behavioral experiment, and with either their right index or right middle finger in the fMRI experiment. We provided the subjects with trial-by-trial feedback only during the training phase, by means of a green or red fixation cross for correct and incorrect responses, respectively. The inter-trial interval was 3000-3500 ms for the behavioral experiment and 3500-5500 for the fMRI experiment. The behavioral experiment consisted of eight blocks of 75 trials (600 trials in total), and the fMRI experiment consisted of ten blocks of 45 trials in two runs (450 trials in total). Summary feedback (percentage correct) was provided to the subject during the break after each block. A training phase preceded the experiment to familiarize the subjects with the task and assess their individual motion coherence threshold at which they performed at 75% correct. There was a resting period of 30 seconds after every block in the fMRI experiment, and a longer resting period between the sessions.

In the fMRI experiment, we also acquired two additional localizer tasks. In the motion

localizer, we presented the same motion stimuli that we used in the experiment (see subsection 2.2.2). The motion coherence level was fixed to 80% and the duration of a trial was 12s. There were ten blocks of seven trials each, presented in pseudorandom order: Upward, downward and random motion in either the LVF or the RVF, and a fixation condition. The subject's task was to press a button when the fixation cross turned from white to orange, to help them fixate at the center of the screen.

In the language localizer, we presented the same word lists that we used in the experiment (see subsection 2.2.2). Subjects were presented with ten blocks of five trials. Each trial consisted of 300 ms presentations of 25 words alternating with 300 ms fixation (15s per trial). Within a trial, all words were from the same category (upward, downward, neutral, letter strings and an additional fixation condition). Participants were instructed to monitor occasional word repetitions (1-back task, occurring on average 3 times per trial). We chose a 1-back task to make sure that participants would attentively read the words. For both localizer tasks, the inter-trial interval was 1 s.

The order of the fMRI sessions was: 1. short training of the task; 2. thresholding procedure; 3. experimental session 1; experimental session 2; language localizer; motion localizer; anatomical T1.

2.2.4. BEHAVIORAL ANALYSIS

We calculated congruency effects for four behavioral measures: Reaction time (RT), percentage correct and signal-detection-theoretic measures *d'* and *C* (Macmillan and Creelman, 2005). *d'* is a measure of a subject's stimulus discriminability, also known as perceptual sensitivity, and was calculated as follows:

$$d' = z(H) - z(F)$$

H denotes the hit rate, F the false alarm rate, and the z transformation converts these measures to a z score (i.e., to standard deviation units). This measure is independent of any potential biases induced by the motion direction suggested by the word. This bias can be analyzed separately by estimating *C*, the internal response criterion of the subject, which was calculated as follows:

$$C = -1/2[z(H)+z(F)]$$

A negative criterion arises when the false alarm rate exceeds the hit rate, and therefore indicates liberal performance in reporting coherent motion during trials that contain no coherent motion in the current experimental setting, whereas a positive criterion denotes conservative reporting. Trials were labeled as congruent when the motion described by the word matched the direction of visual motion, e.g. "rise", followed by a stimulus with upward moving dots. When the motion described by the word and the direction of visual motion did not match, the trial was labeled incongruent. Neutral words were used as a control condition. Trials with RTs that were >3 SD longer/shorter than the individual subject mean RT were excluded from the analyses (in total 2.0%). Each of the four behavioral measures was subjected to a repeated measures analysis of variance, including factors congruency (congruent, incongruent), visual field (LVF, RVF) and experiment (behavioral experiment, fMRI experiment).

2.2.5. fMRI ACQUISITION

Images were acquired on a 1.5 Tesla Avanto MRI system (Siemens, Erlangen, Germany). Whole-brain T2*-weighted gradient-echo echo-planar images (repetition time: 2000 ms, echo time: 40 ms, 33 ascending slices, voxel size: 3x3x3 mm, flip angle: 80 degrees, field of view: 192 mm) were acquired using a 32-channel head coil. A high-resolution anatomical image was collected using a T1-weighted magnetization prepared rapid gradient-echo sequence (repetition time: 2730 ms, echo time: 2.95 ms, voxel size: 1x1x1 mm).

2.2.6. fMRI DATA ANALYSIS

Analysis was performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm, Wellcome Trust Centre for Neuroimaging, London, UK). The first four volumes of each run were discarded to allow for scanner equilibration. Preprocessing consisted of realignment through rigid-body registration to correct for head motion, slice timing correction to the onset of the first slice, coregistration of the functional and anatomical images, and normalization to a standard T1 template centered in MNI space by using linear and nonlinear parameters and resampling at an isotropic voxel size of 2 mm. Normalized images were smoothed with a Gaussian kernel with a full-width at half-maximum of 8 mm. A high-pass filter (cutoff: 128 s) was applied to remove low-frequency signals, such as scanner drift.

The ensuing preprocessed fMRI time series were analyzed on a subject-by-subject basis using an event-related approach in the context of the general linear model. Regressors for the first-level analysis were obtained by convolving the unit impulse time series for each condition with the canonical hemodynamic response function. We modeled the twelve different conditions of the experiment [word type (3) x motion type (2) x visual field (2)] separately for each of the two sessions. Because 'motion type' was varied between subjects (half of the subjects were presented 'upward' and 'random' motion and the other half 'downward' and 'random' motion) we collapsed the conditions over subjects to obtain congruent, incongruent and neutral conditions for both 'coherent' and 'random' motion stimuli for both visual fields. We assessed the effects of congruency between language and perception for the trials that contained coherent motion. Resting periods were modeled as a regressor of no interest. We included six nuisance regressors related to head motion: Three regressors related to translation and three regressors related to rotation of the head. For the localizers, we used the same procedure. Both localizers used a block design. The motion localizer had seven conditions and block duration of 12 s. The language localizer had five conditions and block duration of 15 s.

2.2.7. STATISTICAL ANALYSIS

We used a priori functional information on the basis of the results from the localizers to constrain our search space (Friston et al., 2006). In particular, we isolated the regions that were involved in semantic language processing (language localizer) and visual motion processing (motion localizer). These corresponded to the left middle temporal gyrus (lMTG, language localizer) and bilateral hMT+/V5 (motion localizer).

Specifically, we obtained the anatomical location of the left MTG by contrasting the three word conditions (up, down, neutral words) with the random consonant letter strings condition (MNI coordinates: [-54,-34,4]). We obtained the anatomical location of the right hMT+/V5 ROI by contrasting visual motion stimulation in the LVF > RVF (MNI

coordinates: [40,-78,4]), and the left hMT+/V5 with the reverse contrast (MNI coordinates: [-40,-82,8]). We defined search volumes comprising spheres of 10 mm around these regions and corrected our results for multiple comparisons using a family-wise error rate (FWE) threshold of p<0.05 within this search volume (Worsley, 1996). We computed the mean activity over the voxels in each ROI for the different conditions.

Finally, to verify the language-perceptual interactions that have previously been reported in parietal cortex (Sadaghiani et al., 2009; Tan et al., 2008) we performed an additional ROI analysis with peak coordinates from Sadaghiani et al. (2009) (MNI coordinates: [45,-45,39] and [-42,-54,45]) and Tan et al. (2008) (MNI coordinates: [-61,-32,27]) following the procedure described for the other ROI analyses. Additional whole-brain statistical inference was performed using a cluster-level statistical test to assess clusters of significant activation (Friston et al., 1996). We used a corrected cluster threshold of p<0.05, on the basis of an auxiliary voxel threshold of p<0.001 at the whole-brain level.

2.3. RESULTS

2.3.1. BEHAVIORAL EFFECTS OF LANGUAGE ON MOTION PERCEPTION

Here, we report the combined behavioral data from the behavioral and fMRI experiment. Participants responded faster to the motion stimuli when they were preceded by a congruent motion word than by an incongruent word (congruency: $F_{1,42}$=10.91, p=0.002). Crucially, this congruency effect was modulated by visual field ($F_{1,42}$=4.92, p=0.032; see Figure 2.2A,E)). Motion stimuli that were preceded by congruent motion words were responded to faster when presented in the RVF (congruent: RT=702 ms; incongruent: RT=730 ms; ΔRT=28 ms, $F_{1,42}$=23.59, p<0.001), but not in the LVF (congruent: RT=735 ms; incongruent: RT=744 ms; ΔRT=9 ms, $F_{1,42}$=1.24, p=0.27). The RT effects did not differ between the two experiments (congruency x experiment: $F_{1,42}$<0.01, p=0.98; visual field x congruency x experiment: $F_{1,42}$=0.26, p=0.61) indicating that the congruency effect was larger for RVF than for LVF in both studies. There was also a general right visual field advantage for RTs (visual field: $F_{1,42}$=10.55, p=0.002) which was larger for the fMRI experiment than the behavioral experiment (visual field x experiment: F1, 42=5.29, p=0.026).

Subjects' task performance was individually thresholded using an adaptive staircasing procedure (see section 2.2) to ensure overall approximately 75% correct performance. On average, subjects answered 79% of trials correctly (± 4.2%, mean ± SD) at a motion coherence level of 19% (± 8.5%, mean ± SD). Accuracy was significantly higher for congruent compared to incongruent trials for both visual fields (main effect of congruency: $F_{1,42}$=8.85, p=0.005; LVF: congruent: 76.1%; incongruent: 72.2%; Δ=3.9%, $F_{1,42}$=6.95, p=0.012; RVF: congruent: 81.5%; incongruent: 77.4%; Δ=4.1%, $F_{1,42}$=4.72, p=0.036). There was no significant interaction between congruency and visual field ($F_{1,42}$=0.01, p=0.92; see Figure 2.2B,F). The effects were similar in the two experiments (congruency x experiment: $F_{1,42}$=0.05, p=0.83; visual field x congruency x experiment: $F_{1,42}$=0.08, p=0.79). Accuracy was higher in the RVF than in the LVF in the imaging experiment (visual field x experiment: $F_{1,42}$=3.01, p=0.090).

Subjects exhibited a more liberal decision criterion when the motion word and visual motion stimulus were congruent than when they were incongruent for both visual fields

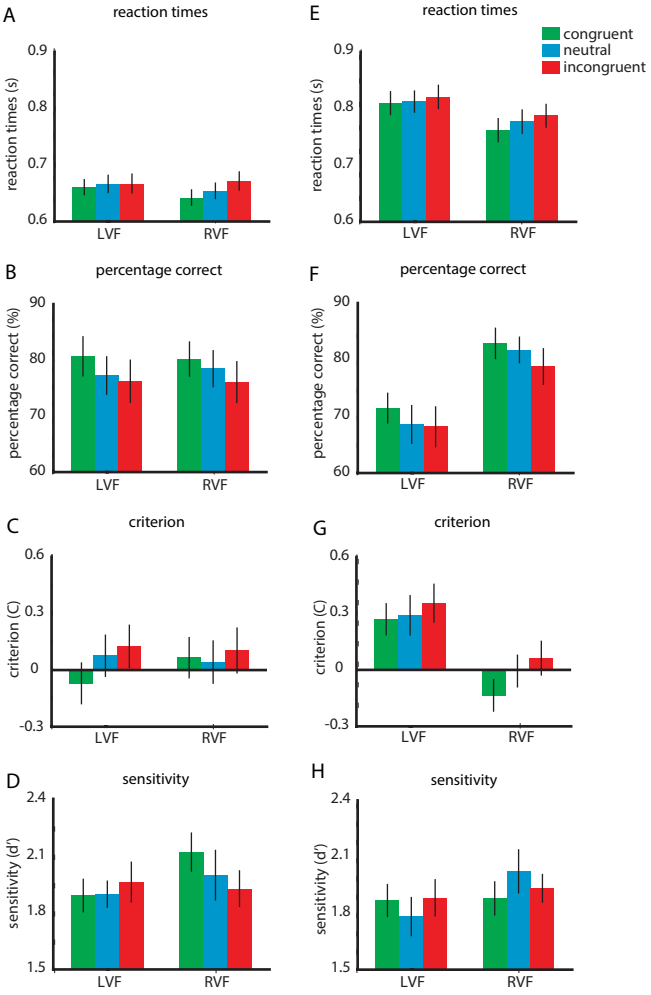

Figure 2.2: Behavioral results. (A–D) Behavioral study. (A) Mean RTs (in s) for visual motion stimuli that were presented in the LVF (left bars) or RVF (right bars) and which were preceded by a congruent (green), neutral (blue), or incongruent (red) word (n = 22). (B) Percentage correct. Other conventions as in A. (C) Decision criterion (*C*). (D) Sensitivity (*d'*). (E–H) fMRI study. Conventions as in A–D.

(main effect of congruency: $F_{1,42}$=11.10, p=0.002; LVF: congruent: C=0.10; incongruent: C=0.24; ΔC=0.14, $F_{1,42}$=9.80, p=0.003; RVF: congruent: C=-0.03; incongruent: C=0.08; ΔC=0.11, $F_{1,42}$=6.02, p=0.018). No significant interaction between congruency and visual field was present ($F_{1,42}$=0.20, p=0.66; see Figure 2.2C,G). Only for criterion, there was a significant difference in the lateralization of the congruency effects between the experiments (visual field x congruency x experiment: $F_{1,42}$=6.89, p=0.012) which is caused by the fact that the more liberal criterion for congruent stimuli is stronger in the LVF during the behavioral experiment but stronger in the RVF during the imaging experiment.

Participants were more conservative in their perceptual decisions in the LVF than in the RVF in the fMRI experiment (visual field x experiment: $F_{1,42}$=4.73, p=0.035).

Sensitivity for motion detection was neither different for congruent compared to incongruent trials in the LVF nor in the RVF (main effect of congruency: $F_{1,42}$=0.06, p=0.81; LVF: congruent: d'=1.88; incongruent: d'=1.92; $\Delta d'$=-0.04 $F_{1,42}$=0.31, p=0.58; RVF: congruent: d'=2.00; incongruent: d'=1.93; $\Delta d'$=0.07, $F_{1,42}$=1.03, p=0.32), and there was no significant interaction between congruency and visual field ($F_{1,42}$=1.46, p=0.23; see Figure 2.2D,H). There was no difference in sensitivity effects between the experiments (congruency x experiment: $F_{1,42}$=0.73, p=0.40; visual field x congruency x experiment: $F_{1,42}$=2.65, p=0.11).

We included a neutral (no motion) words condition to aid the interpretation of the congruency effects. The neutral condition showed behavior that was intermediate between the congruent and incongruent conditions for RT, accuracy and criterion, suggesting that the motion words could incur either a cost or benefit, depending on the congruency with the upcoming motion stimulus (RT: congruent > neutral LVF: T_{43}=-0.77, p=0.45; RVF: T_{43}=-2.63, p=0.012; neutral > incongruent LVF: T_{43}=-0.75, p=0.46; RVF: T_{43}=-2.71, p=0.010; accuracy: congruent > neutral LVF: T_{43}=2.24, p=0.031; RVF: T_{43}=1.04, p=0.30; neutral > incongruent LVF: T_{43}=0.51, p=0.62; RVF: T_{43}=1.88, p=0.067; criterion: congruent > neutral LVF: T_{43}=-1.94, p=0.059; RVF: T_{43}=-1.21, p=0.23; neutral > incongruent LVF: T_{43}=-1.73, p=0.091; RVF: T_{43}=-1.62, p=0.11; sensitivity: congruent > neutral LVF: T_{43}=0.63, p=0.53 RVF: T_{43}=-0.14, p=0.89; neutral > incongruent LVF: T_{43}=-1.12, p=0.27; RVF: T_{43}=0.96, p=0.34).

2.3.2. NEURAL EFFECTS OF LANGUAGE ON MOTION PERCEPTION

As expected, motion stimuli in the LVF were associated with increased activity in the right hMT/V5+, whereas motion stimuli in the RVF led to stronger responses in the left hMT/V5+ (difference between ipsilateral and contralateral visual stimuli, lhMT+/V5: T_{21}=8.39, p<0.001; rhMT+/V5: T_{21}=8.76, p=<0.001; see Figure 2.3C-D). However, hMT+/V5 was not modulated by the congruence between the motion word and the visual motion stimulus, not even at liberal statistical thresholds (p>0.05 uncorrected). An effect of language on motion perception was observed however in the left middle temporal gyrus (lMTG, MNI coordinates: [-58,-34,-6]), where we found a significant increase in activation for the congruent compared to the incongruent condition (See Figure 2.3A-B, T_{21}=4.17, p=0.029). The size of the congruency effect was not different for LVF compared to RVF stimuli in lMTG. Finally, there was a borderline significantly larger activation for the congruent than the incongruent condition in left anterior IPS (T_{21}=3.61, p=0.050).

We also carried out a whole-brain analysis, to identify potential other regions that are modulated by the congruency between the motion word and motion stimulus. No other brain regions showed a significant difference in activation for the incongruent condition relative to the congruent condition, nor a significant interaction between congruency and visual field.

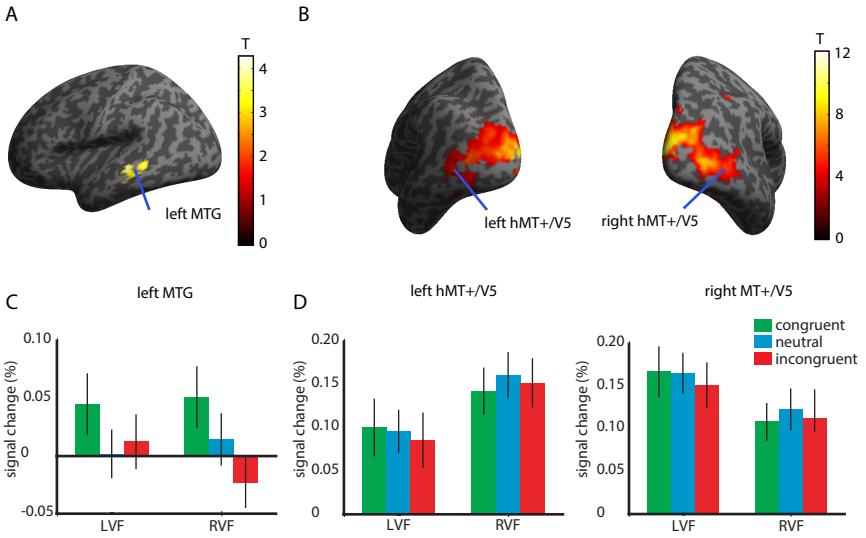

Figure 2.3: fMRI results. (A) Activation for congruent > incongruent conditions plotted on an inflated render MNI brain. The only significant modulation because of congruency is localized in lMTG (n = 22). (B) Activation in the motion localizer for motion > fixation plotted an inflated render MNI brain. (C) Within the lMTG blob (p<0.001 uncorrected) the percentage signal change for the congruent (green), neutral (blue), and incongruent (red) conditions is plotted for both the LVF (left) and RVF (right). (D) For both hMT+/V5 ROIs, the percentage signal change for the congruent (green), neutral (blue), and incongruent (red) conditions is plotted. There is no modulation of either left or right hMT+/V5 by congruency, but there is a clear activation difference in both ROIs between stimuli presented in the LVF and RVF.

2.4. DISCUSSION

We investigated the effects of motion language on motion perception in a combined behavioral and fMRI study. We found that when motion words were congruent with the direction of the visual motion stimulus, subjects were faster, more accurate, and more liberal in detecting visual motion. Interestingly, the speed benefit was present only for visual stimuli that were presented in the RVF, and thus processed in the left (language dominant) hemisphere. We observed a potential neural counterpart to these behavioral facilitatory effects in the left middle temporal gyrus, an area involved in lexical knowledge. This suggests that semantic categorization may be an integral part of the perceptual decision process, and lMTG a neural locus where language and perception interact.

Previous work already suggested an effect of motion words on motion perception. Meteyard et al. (2007) investigated whether a stream of auditorily presented motion words affected the detection of motion in centrally presented visual stimuli. They showed that when motion stimuli were paired with congruent motion words, motion sensitivity (d') was improved and decision criterion was more liberal. Despite the substantial differences in design (e.g. trial-by-trial presentation of words vs. blocked presentation, visual presentation vs. auditory presentation), we partly replicate and extend these findings, by showing modulations of accuracy, criterion and reaction times.

Interestingly, a variation of the Meteyard et al. (2007) study by Pavan et al. (2013) showed a double dissociation between discrimination sensitivity and reaction times depending on whether motion coherence was above or at threshold. With suprathreshold motion, responses were faster for congruent stimuli, but sensitivity was equal across conditions. When the motion was at threshold however, sensitivity was higher for congruent stimuli, but responses were equally fast across conditions. Thus, differences in motion coherence level might explain the absence of sensitivity effects in our study, and the lack of RT effects in the study of Meteyard et al. (2007). Another determinant of the nature of language-perception interactions might be the degree of temporal overlap between linguistic and perceptual information. In our study, the two events were separated by 300 ms, which might result in integration at a later stage in the decision process.

Interestingly, the reaction time effects were dependent on the visual field in which the motion stimuli were presented: Only for motion stimuli that were presented in the right visual field (which are processed by the language-dominant left hemisphere), we observed faster reaction times when the motion stimuli were preceded by congruent, compared to incongruent, motion words. This lateralization of a language-perception interaction has been previously observed for other types of visual stimuli (e.g., color, objects) (Drivonikou et al., 2007; Gilbert et al., 2006, 2008; Mo et al., 2011; Zhou et al., 2010). The lateralization effect we find in our study supports the hypothesis that language changes perception in a specific way, i.e., by a process in which word meaning is matched with the outcome of a semantic categorization of visual stimuli (e.g., "rise" matches with visual motion categorized as moving 'upwards'). This appears fundamentally different from more general priming or response conflict effects that do not depend on stimulus hemifield, such as those observed in e.g. Stroop paradigms (Leung et al., 2000). Related, the results are unlikely to be caused by attentional cueing, as the word cue had no probabilistic relationship with the following stimulus (direction of movement of visual motion). Furthermore, it is difficult to see why attentional cueing would only be present for stimuli that are presented in the right visual field.

With our fMRI study we aimed to elucidate which neural regions were sensitive to the congruency between the motion words and visual stimuli. Such a congruency effect was observed in the left middle temporal gyrus, although the congruency effect was not significantly stronger for motion presented in the right visual field (as was the case for the behavioral congruency effect). The lMTG is part of the mostly left-lateralized language network and is known to be involved in both lexical retrieval including word semantics and multisensory processing and integration (Beauchamp et al., 2004; Hagoort et al., 2009; Menenti et al., 2011; Noppeney et al., 2008; Schneider et al., 2008). Similar to our finding that the lMTG shows increased activity for congruent compared to incongruent conditions, Schneider et al. (2008) showed a crossmodal priming effect in response to semantically congruent stimuli in the lMTG, using EEG. They suggest that the enhanced gamma-band power for congruent compared to incongruent conditions may reflect a crossmodal semantic matching process that is triggered by the expectation of an upcoming event (i.e., a congruent stimulus). This crossmodal matching process may also occur when making perceptual decisions, if the perceptual decision is translated into a lexical concept.

In a ROI-based post-hoc test with peak coordinates from Sadaghiani et al. (2009),

a cluster in left anterior IPS was also sensitive to the difference between congruent and incongruent linguistic and perceptual information, in line with previous studies (Sadaghiani et al., 2009; Tan et al., 2008).

Surprisingly, we did not find any interaction effects in motion-sensitive visual cortical area hMT+/V5. This is in contrast to earlier studies that have found neural activity modulations by linguistic stimuli during perceptual tasks that occurred early in time and was localized in sensory areas (Hirschfeld et al., 2011; Mo et al., 2011; Thierry et al., 2009). One potential reason for this discrepancy could be the fact that subjects were instructed to ignore the motion words, which may have attenuated processing of the verbal material.

How do these behavioral and neural results inform the central question: At which level of processing does the interaction between language and perception occur? We conjectured two levels at which this interaction could occur. First, motion words could induce an 'automatic prediction' about visual motion, thereby automatically recruiting the relevant sensory areas. Alternatively, but still in line with the sensory level hypothesis, motion words themselves may recruit the motion-sensitive visual cortex, as advocated by the embodied language hypothesis. This hypothesis claims that words describing motion are partly represented in the corresponding perceptual areas that process the actual visual stimuli the words describe (Barsalou, 2008). However, in our study we did not find evidence for engagement of hMT+/V5 or nearby sensory areas in the interaction between motion words and motion perception. Thus, our data do not support strong versions of embodiment according to which motion words automatically and necessarily activate visual motion areas.

Second, the interaction between language and perception could occur at a higher level of language processing. The visual motion stimuli might be conceptually categorized ('up', 'down'), as the participants are required to make a categorical perceptual decision. So even though it is not necessary to perform the task, linguistic representations may be automatically activated (Tan et al., 2008). If the activated motion word meaning matches the subsequent semantic representation activated by the visual motion stimulus, this then leads to more activity in lMTG (Schneider et al., 2008), as well as improved behavioral performance. Klemfuss et al. (2012) support this interpretation of the linguistic effects on perception by showing that the language effects may be post-perceptual rather than directly influencing early perceptual processing. In a visual search experiment, they demonstrate that the disruption of visual search by automatically activated irrelevant linguistic information is the result of an interaction at a response-selection stage of processing. Thus, semantic categorization may be an integral part of the perceptual decision process. This hypothesis is in line with both the behavioral data (showing reaction time and criterion effects) and the fMRI data (showing post-perceptual integration effects of the semantic and visual information in the lMTG).

In the current study, motion words influenced motion perception despite the fact that the words had no predictive value for the upcoming stimulus and subjects were instructed to ignore them. This suggests that the influence of language on perception is an automatic rather than a strategic process. However, the experimental effects were modest and 'local' (i.e., only visible when the linguistic and visual stimuli were processed in the same hemisphere) compared to other studies, which suggests that a stronger context may be necessary for more robust and widespread language-perceptual interactions.

For instance, Lupyan and Ward (2013) found that the presentation of a valid verbal cue before an invisible image of an object changed object detection performance relative to an uninformative cue. This suggests that attended and predictive language can exert a strong influence on perception. Furthermore, when the linguistic context is stronger, i.e. when stimuli are sentences or narratives describing motion, studies have found activation of motion processing areas more proximal to MT+ (Saygin et al., 2010; Wallentin et al., 2011).

The unattended nature of the motion words in our study (as a consequence of the task difficulty of the motion detection task and the task instructions) may be an explanation for the 'local' effects of motion words on motion perception, in terms of neural activation and reaction times: Motion words influenced RTs only for stimuli presented in the RVF. In these trials, the linguistic and visual material was processed within the same (left) hemisphere. Given that attention is often thought to have a 'broadcasting' effect (Dehaene and Naccache, 2001; Dehaene et al., 2003), it is an interesting question whether attention to the words would result in congruency effects on reaction times also for visual material presented to the LVF and possibly to a more extended network of areas in the parietal and prefrontal cortex that are involved in the 'broadcasting' of information (Dehaene and Changeux, 2011). This hypothesis would provide an alternative explanation for the often reported, but debated, observation that language exerts stronger effects on RVF than on LVF stimuli. This asymmetry is thought to be related to the left-lateralization of the language system (Gilbert et al., 2006; Klemfuss et al., 2012; Regier and Kay, 2009) but importantly, the crucial factor could be the degree to which the linguistic information is attended, and thus broadcasted. Therefore, when the motion words are attended, we expect larger and potentially bilateral effects. This prediction could be tested in future experiments.

In conclusion, this study provides insight into the behavioral and neural effects of language on perception. We show that language affects motion perception, with stronger effects for motion stimuli that are processed in the language-dominant left hemisphere. These interactions are neurally mediated by 'language areas' rather than perceptual areas, suggesting that these may form integral part of the network involved in perceptual decisions about visual motion stimuli.

2.5. SUPPLEMENTARY MATERIALS

Table 2.1: Dutch word lists (with English translation) for upward, downward and neutral words. Words are ordered alphabetically.

Up (Dutch)	English translation	Down (Dutch)	English translation	Neutral (Dutch)	English translation
bestijgen	mount	afdalen	descend	aanraken	touch
heffen	lift	afglijden	slide down	beheren	manage
klauteren	clamber	afzakken	come down	bivakkeren	lodge
klimmen	climb	bezinken	settle down	boenen	polish
lanceren	launch	bukken	stoop	dichtnaaien	sew up
omhooggaan	go up	dalen	descend	fatsoeneren	model
omhoogkomen	come up	druipen	drip	filmen	film
opgaan	go up	duiken	dive	happen	bite
opgooien	throw up	gieten	pour	imiteren	imitate
ophijsen	pull up	instorten	collapse	kamperen	camp out
ophogen	raise	inzinken	break down	liplezen	lip-reading
opklimmen	climb	kieperen	tumble	markeren	mark
opkrikken	jack up	neerdalen	go down	meubileren	furnish
oplaten	launch	neergaan	go down	printen	print
oprijzen	rise	neerhalen	take down	ratelen	rattle
opstaan	stand up	neerkletteren	crash	rommelen	rumble
opstijgen	ascend	neerkomen	fall upon	rondvragen	ask
opstuwen	drive	neerploffen	plump down	scheren	shave
optillen	lift	neerstorten	crash	smullen	feast
opvliegen	fly up	neervallen	fall down	spieken	copy
rijzen	rise	storten	fall	troosten	comfort
stapelen	pile up	tuimelen	tumble	uitslapen	sleep late
stijgen	rise	verlagen	lower	verstoren	disturb
verrijzen	arise	zakken	drop	wassen	wash
zwellen	swell	zinken	sink	wegen	weigh

3

MANIPULATING WORD AWARENESS DISSOCIATES FEED-FORWARD FROM FEEDBACK MODELS OF LANGUAGE-PERCEPTION INTERACTIONS

Jolien C. FRANCKEN, Erik L. MEIJS, Odile M. RIDDERINKHOF, Peter HAGOORT, Floris P. DE LANGE, and Simon VAN GAAL

Previous studies suggest that linguistic material can modulate visual perception, but it is unclear at which level of processing these interactions occur. Here we aim to dissociate between two competing models of language-perception interactions: A feed-forward and a feedback model. We capitalized on the fact that the models make different predictions on the role of feedback. We presented unmasked (aware) or masked (unaware) words implying motion (e.g., "rise", "fall"), directly preceding an upward or downward visual motion stimulus. Crucially, masking leaves intact feed-forward information processing from low- to high-level regions, whereas it abolishes subsequent feedback. Under this condition, participants remained faster and more accurate when the direction implied by the motion word was congruent with the direction of the visual motion stimulus. This suggests that language-perception interactions are driven by the feed-forward convergence of linguistic and perceptual information at higher-level conceptual and decision stages.

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3.1. INTRODUCTION

A growing body of evidence shows that language affects perception (e.g., Landau et al., 2010; Lupyan, 2012a; Meteyard et al., 2007; Thierry et al., 2009; Winawer et al., 2007). However, it is unclear whether linguistic material changes information processing at low-level sensory stages (perceptual level) or whether these 'language-perception interactions' are mediated by effects at higher cognitive levels of representation (conceptual level) or even at later perceptual decision stages. Here, we refer to perception as encompassing both the raw sensory processing of a visual stimulus as well as the transformation of this event into a categorical decision. In this study, we aim to dissociate between two models that favor low-level versus higher-level interactions, respectively.

In the first model, which we call the 'feedback model' (Figure 3.1A), linguistic information is processed in language-specific regions and then feeds back, or is 'broadcasted' to lower-level sensory regions to modulate perceptual information processing. For instance, the activation of the semantic representation of the motion-implying word "rise" in the temporal cortex may feedback and affect the sensory representation or processing of visual motion stimuli (i.e., moving dots) in hMT+/V5. This feedback model is one of the dominant views in the field (Lupyan, 2012a; Meteyard et al., 2007). In line with this model, and the view that language comprehension reflects an 'embodied process' (Barsalou, 2008), words or sentences describing motion have been shown to activate motion-sensitive visual areas that process actual visual motion (Saygin et al., 2010). Similarly, predictive processing theories have proposed that motion words may induce an 'automatic top-down prediction' about visual motion, thereby automatically recruiting hMT+/V5, in a way that is similar to how expectation affects visual perception (Hirschfeld et al., 2011; Lupyan, 2012a; Summerfield and de Lange, 2014). However, these theories are yet to be experimentally verified.

Alternatively, according to the second model language might influence perception at a later conceptual or decision stage rather than at the sensory stage, which is illustrated by the 'feed-forward model'. To illustrate, in this model the motion word "rise" is processed in language-specific regions as well, where it activates its conceptual representation. The visual motion information is first processed in motion-sensitive area hMT+/V5 and subsequently up to a more conceptual level ('up'/'down'). Then, this conceptual representation of the visual stimulus interacts with the conceptual representation of the motion word. In this model, language modulates perception not by directly affecting the sensory processing stage in a top-down manner, but because visual information converges on the same conceptual representation as semantic information. This view is supported by recent neuroimaging evidence (Francken et al., 2015a; Klemfuss et al., 2012; Tan et al., 2008): For example, we have recently shown that the congruency of word-visual motion pairs (e.g., the word "rise" and upward visual motion) is reflected only in higher-order areas (left middle temporal gyrus (lMTG)), with activity in sensory visual areas (hMT+/V5) unchanged (Francken et al., 2015a).

In sum, there is empirical support for both the feedback and the feed-forward model of language-perception interactions. Here we present an experimental procedure that allowed us to directly compare key predictions of the two models. Crucially, we manipulated the awareness level and thereby the nature of processing of the linguistic information by means of backward masking. Backward masking is a well-known experimental proce-

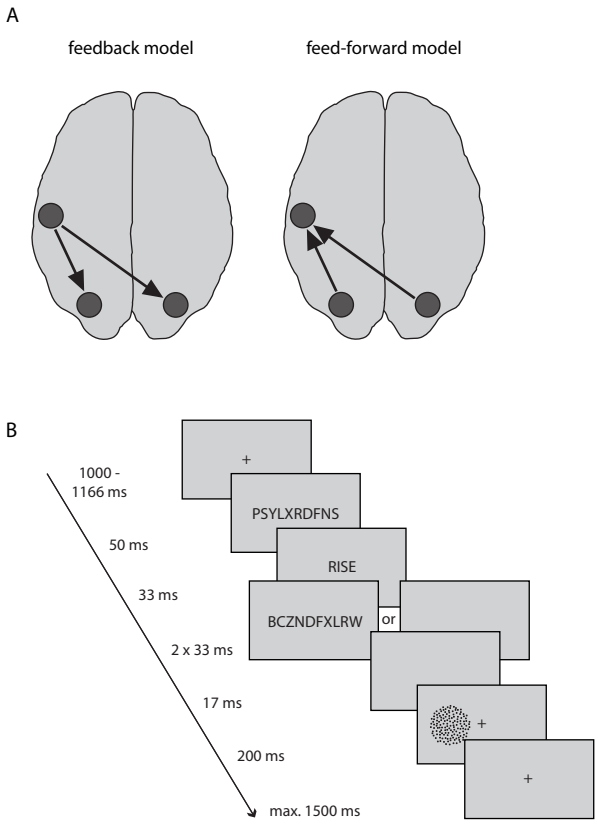

Figure 3.1: Models and task design. (A) In the feedback model of language-perception interactions (left), linguistic information is processed in language-specific regions and subsequently feeds back to the sensory system to modulate perceptual processing. Therefore, the processing of visual stimuli is influenced at the level of visual cortex. In the feed-forward model of language-perception interactions (right), linguistic information is likewise processed in language-specific regions where it activates a conceptual representation. Crucially, in this case, the visual information is also processed up to a conceptual level, and it is here at the conceptual level that linguistic information interacts with visual stimuli. (B) A congruent or incongruent motion word (upward or downward, e.g., "rise", or "fall") is displayed in advance of every motion discrimination trial. All words are preceded by a forward mask; unaware words are additionally followed by two backward masks. The visual motion stimulus is presented either in the left or right lower visual field and the dots move upward or downward.

dure to render briefly presented stimuli unaware by interspersing it with visual masks. Influential models of awareness in monkey electrophysiology (Lamme et al., 2002) and human imaging studies (Del Cul et al., 2007; Fahrenfort et al., 2007) suggest that backward masking selectively disrupts feedback processing, while leaving feed-forward processing relatively intact (Lamme and Roelfsema, 2000; van Gaal and Lamme, 2012). Because backward masking selectively disrupts feedback processing, this experimental design allowed us to adjudicate between the feed-forward and feedback model of language-perception interactions. Here, masking disrupts the feedback, sometimes also referred

to as 'broadcasting' (Dehaene and Changeux, 2011), of the linguistic information from language areas in the left temporal lobe to sensory areas involved in word processing as well as sensory areas related to processing of the visual motion stimulus. Since we explore the effects of language on motion perception, we here refer to the latter type of feedback. Thus, the feedback model predicts that masking words will abolish the perceptual effect. In contrast, the feed-forward model predicts that masked words will still affect perception because these effects are supported by feed-forward processing to higher-level conceptual regions only.

Besides this main question, we had two additional questions. First, we were interested in the potential lateralization of (unaware) language-perception interactions. Previous studies have indicated that these interactions might be larger, or exclusively present, for visual information processed in the language-dominant left hemisphere (Francken et al., 2015a; Gilbert et al., 2006), although evidence is mixed (Witzel and Gegenfurtner, 2011). Therefore, we explored potential differences in lateralization effects between unmasked and masked words by presenting motion stimuli in the left and right hemifield.

Second, we wondered whether and how decision and control processes that evolve after the actual integration of perceptual and linguistic information might differ between unmasked and masked conditions. Since the motion words refer to upward and downward motion directions, control processes might become activated to suppress this information which might interfere with the motion discrimination task. Previous studies of response conflict (i.e., Stroop or flanker tasks) show that control mechanisms become activated with increasing response time (Jiang et al., 2013; Ridderinkhof, 2002). However, at present, it is undecided whether these mechanisms are dependent on awareness of the (in)congruency of the stimulus or whether masked stimuli can evoke these conflict-control mechanisms as well (Kunde et al., 2012).

3.2. MATERIALS AND METHODS

3.2.1. PARTICIPANTS

Thirty-eight healthy, right-handed participants with normal or corrected-to-normal vision (2 males, 36 females; age range: 18-29 years) took part in the two sessions of this experiment. All participants were native Dutch speakers and reported having no reading problems. The study was approved by the regional ethics committee and a written informed consent was obtained from the participants according to the Declaration of Helsinki. Compensation was 25 Euros, or course credit.

3.2.2. STIMULI

Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997) within MATLAB (MathWorks, Natick, MA, US), and displayed on an ASUS LCD computer monitor (refresh rate: 60 Hz, resolution: 1920 x 1080, size: 50.9 x 28.6 cm). Stimuli were presented in white on a light-gray background. The visual random-dot motion (RDM) stimuli consisted of white dots (density: 2.5 dots/deg; speed: 6.0 deg/s) plotted within a circular aperture (radius: 7.5 deg). On every trial, the RDM stimulus was presented on either the left or right side of the screen (8.5 deg horizontal eccentricity from fixation to centre of circular aperture) for 200 ms. In the first frame of the RDM stimulus, a random configuration of

dots was presented within the annulus. Subsequently, on every frame a certain percentage of the dots was replotted consistently in one direction (upward or downward) on the next frame (see subsection 3.2.3). Dots moving outside of the annulus and other remaining dots were replotted at a random location within the annulus.

Five verbs describing each direction of motion (in Dutch, here translated to English; upward: *grow, ascend, rise, climb, go up*; downward: *sink, descend, drop, dive, go down*), and ten no motion verbs (*bet, mourn, exchange, glow, film, rest, cost, sweat, wish, relax*) were used in the experiment. Motions words and neutral words were matched for lexical frequency (taken from the CELEX database) and word length (5-8 letters)(both p>0.2). Masks were randomly generated combinations of ten consonant strings. Both words and masks were presented at the center of the screen, using capital letters in a mono-spaced font.

3.2.3. PROCEDURE

Participants performed a motion discrimination task (upward vs. downward motion) on a visual RDM stimulus (see Figure 3.1B). A central fixation cross (width: 0.4 deg) was presented throughout the trial, except when a word, mask or blank screen was presented. Each trial started with a centrally presented forward mask (50 ms) followed by a word (33 ms), which could either be a motion word or a no motion (neutral) word. Presentation of the words was pseudorandom within each block of the experiment. Awareness of the word was manipulated by presenting either backward masks (2 x 33 ms; unaware condition) or a blank screen (67 ms; aware condition) after word presentation. A short inter-stimulus interval (ISI) of 17 ms was always present after either of these screens. Next, a visual RDM stimulus was presented (200 ms) in either the left visual field (LVF) or in the right visual field (RVF). Participants had to indicate as quickly and accurately as possible whether the RDM contained upward or downward motion, while maintaining fixation at the central cross. The brief presentation time of the RDM stimulus served to minimize the chance of eye movements to the stimulus, as saccade latencies are in the order of 200 ms (Carpenter, 1988). Participants were instructed to respond as quickly and accurately as possible by pressing a keyboard button with either the index or middle finger of the right hand (counterbalanced across participants). The inter-trial interval (ITI) was 1000-1166 ms.

In 10% of the trials the motion discrimination task was followed by an additional task assessing the visibility of the words. Here, participants indicated whether the word presented earlier in the trial was a motion or a no motion word. These catch trials were included for two reasons. First, they ensured attention to the words, which enhances processing of the primes in both unmasked and masked conditions (Naccache et al., 2002; Spruyt et al., 2012). Second, catch trials were used to estimate word awareness. Participants were instructed to always respond to the catch question. They were explicitly told that there was a fifty percent chance of either motion or no motion words (10 different words of each category) in the catch trials. Note that no motion words were solely included to test for the visibility of the words.

The experiment consisted of two one-hour sessions on separate days within one week. In the first session participants performed a training phase to familiarize them with the task and assess their individual motion coherence threshold at which they performed

the motion discrimination task at 75% correct. Participants first practiced the motion discrimination task in three blocks with fixed coherence levels (80%, 55%, and 30% respectively). The coherence level of the next training block was adjusted on the basis of performance in the previous blocks. The coherence level after the fourth training block was taken as the starting point for the Bayesian adaptive staircase procedure (Watson and Pelli, 1983), which was run separately for LVF and RVF stimuli. This was done to yield comparable task difficulty and performance in both visual fields and for all participants. The threshold for discrimination was defined as the percentage of coherent motion for which the staircase procedure predicted 75% accuracy. In both the remaining training blocks and the experiment, the coherence level was fixed within a block. The same Bayesian staircase procedure ran throughout the block, however the actual coherence level was updated only between blocks (based on the estimate after the last trial of a block), to accommodate potential practice and fatigue effects over the course of the experiment. In the final training blocks, participants practiced the discrimination task while the words were presented and the catch task was added.

During training, we provided participants with trial-by-trial feedback for both the motion task (except for the threshold estimation block) and the catch trial task by means of a green or red fixation cross for correct and incorrect responses, respectively. The training was followed by a practice phase, in which participants completed 440 trials (5 blocks of 88 trials) of the actual experimental task to familiarize them with the task and to avoid practice effects in the actual experimental blocks. On the second day, participants first completed a short training (88 trials). The experiment on the second day consisted of ten blocks of 80 trials (800 trials in total). All analyses reported here are based on the ten experimental blocks in this final session. Summary feedback (percentage correct) was provided during the break after each block.

One participant was excluded because performance on the unmasked trials of the motion discrimination task was <60% correct. Therefore, analyses were performed on 37 participants.

3.2.4. STATISTICAL ANALYSIS

We calculated congruency effects for reaction times (RT) on correct trials and error rates (ER). On congruent trials, the motion described by the word matched the direction of visual motion, e.g. "rise" followed by a stimulus with upward moving dots. On incongruent trials, the motion described by the word and the direction of visual motion did not match. Missed trials and trials with RTs that were >3 SD than the individual subject mean RT were excluded from the analyses (in total 2.3%). Each of two behavioral measures was subjected to a repeated measures analysis of variance (rm-ANOVA), including factors Congruency (congruent, incongruent), Awareness (aware, unaware) and Visual Field (LVF, RVF).

To further assess the potentially different effects of unmasked and masked words on motion perception, we used Bayesian Statistics (Jeffreys, 1961; Rouder et al., 2009) and delta plots (Ridderinkhof, 2002). Previous studies have indicated that language-perception interactions might be larger, or exclusively present, for visual information processed in the language-dominant left hemisphere (Francken et al., 2015a; Gilbert et al., 2006), while others have failed to replicate these effects (Witzel and Gegenfurtner, 2011).

To differentiate between the presence and absence of evidence for the null hypothesis (no lateralization of congruency effects), we calculated Bayes Factors (BF). BFs express evidence ratios between hypotheses, and therefore provide direct information about the relative likelihood of the alternative vs. the null hypothesis. A BF of 1 indicates no preference for either the null or the alternative hypothesis, and in large samples BF will converge to either 0 or infinity when the null or alternative hypothesis is true respectively (Rouder et al., 2009). By convention a BF likelihood ratio of >3/1 provides moderate evidence for the alternative hypothesis, >10/1 provides strong evidence for the alternative hypothesis, and >30/1 provides very strong evidence for the alternative hypothesis (Jeffreys, 1961). Equivalently, a BF of <1/3 provides moderate support for the null hypothesis, <1/10 provides strong support for the null hypothesis and <1/30 provides very strong support for the null hypothesis. BF ratios between 1/3 and 3/1 provide no evidence for either the null or the alternative hypothesis.

Second, we wondered whether decision and control processes might become activated with increasing response time to suppress the interference of the task-irrelevant linguistic information with the motion discrimination task. Therefore, we calculated delta plots (reflecting the RT congruency effects for different RT bins) and conditional accuracy functions (reflecting the ER congruency effects for different RT bins) to assess the congruency effects across the response time distribution. For each visibility condition, every participant's trials (correct trials only) were sorted on RT and subsequently equally divided over ten RT bins (separate bins for congruent and incongruent trials). Next we performed an rm-ANOVA including factors Congruency (congruent, incongruent), Awareness (aware, unaware) and RT bin (1 to 10). Previous studies show that the build-up of suppression of interference is maximal at the slowest RT bins (Forstmann et al., 2008; Jiang et al., 2013; Ridderinkhof, 2002). Therefore, we performed additional planned paired t-tests on RTs between the first (second minus first RT bin) and last (tenth minus ninth RT bin) slopes to assess whether conflict control became stronger over response time in the current study as well. The strength of automatic response activation by the motion words is inferred from the pattern of errors present at the fastest RT bins. Stronger response capture is associated with a higher percentage of fast errors (Ridderinkhof, 2002). Thus, the critical measure for conflict control effects on ERs was the presence of a three-way interaction between congruency, awareness and RT bin.

To assess the awareness of the words, we calculated the accuracy and *d'* in the catch trials. Percentage correct was defined as the percentage of trials on which participants correctly indicated whether the word was a motion word or not. *d'* is an unbiased measure of the discriminability sensitivity of the observer (Macmillan and Creelman, 2005). *d'* for the unmasked and masked conditions were first compared to each other using paired t-tests and subsequently compared with zero using one-sample t-tests. Following this, we used the accuracy in binomial tests to determine for every participant whether performance was above chance (50% correct). In addition, we calculated correlations between *d'* and congruency effects. We used a regression approach, referred to as Greenwald's method (Greenwald et al., 1995) to test whether the reported congruency effects were still significant when discrimination performance was extrapolated to zero visibility (*d'*=0) (see Greenwald et al. (1995) and Hannula et al. (2005) for further discussion and justification of this method). Finally, we split the participants into a low visibility (*d'*<median) and a

high visibility (*d'*>median) group and we performed an rm-ANOVA across the masked conditions with the factors Congruency (2) and Group (2) to test for potential differences between the congruency effects (CE) of the low and high visibility groups.

3.3. RESULTS

3.3.1. WORD DISCRIMINABILITY

We excluded four out of 37 participants whose discrimination performance of the masked words was above chance-level (binominal test, p<0.1), because for these four participants we could not be sure that they were unable to discriminate the masked words. On a group level (for the remaining 33 participants), the discriminability of the words (motion vs. no motion) was markedly lower when the words were masked (unaware condition) than when they were not masked (aware condition) (difference T_{32}=10.22, p<0.001; unaware *d'*=0.16, corresponding to 52.8% correct responses, T_{32}=2.57, p=0.015; aware *d'*=2.25, 84.0% correct, T_{32}=11.11, p<0.001). To assess whether residual visibility of the masked motion words is responsible for any of the effects on visual motion perception, we performed several control analyses (see subsection 3.3.4).

3.3.2. DO MASKED MOTION WORDS AFFECT VISUAL MOTION PERCEPTION?

We first focus on the effects of word awareness on word-motion congruency. Participants responded faster to the motion stimuli when they were preceded by a congruent motion word than by an incongruent motion word (main effect of congruency: $F_{1,32}$=80.11, p<0.001). This congruency effect was modulated by word awareness (congruency x awareness: $F_{1,32}$=46.20, p<0.001), indicating that the difference between congruent and incongruent conditions was larger when the words were unmasked than when they were masked. Crucially, however, the congruency effect was present both when the words were unmasked (congruent: RT=335 ms; incongruent: RT=395 ms; Δ RT=60 ms, $F_{1,32}$=69.60, p<0.001; see Figure 3.2A), and when they were masked (congruent: RT=350 ms; incongruent: RT=356 ms; Δ RT=6 ms, $F_{1,32}$=6.77, p=0.014).

The congruency effects in error rates go in the same direction for both unmasked and masked words. On average, participants answered 81.3% of trials correctly (± 6.7%, mean ± SD) at an average motion coherence level of 48.1% for the LVF (± 18.3%, mean ± SD) and 46.5% for the RVF (± 16.3%, mean ± SD). Participants made fewer errors for congruent compared to incongruent trials (main effect of congruency: $F_{1,32}$=130.19, p<0.001; aware: congruent: 11.3%; incongruent: 26.9%; Δ ER=15.6%, $F_{1,32}$=126.34, p<0.001; unaware: congruent: 17.8%; incongruent: 19.9%; Δ ER=2.1%, $F_{1,32}$=10.89, p=0.002; see Figure 3.2B). Again, the congruency effect was larger for unmasked words than for masked words (congruency x awareness $F_{1,32}$=81.30, p<0.001).

The word discrimination trials, interspersed throughout the experiment, revealed that performance (visibility) was low for masked words (52.8% correct responses). However, on a group level, visibility was higher than chance level. Therefore, to check whether incidental word visibility might have been responsible for the observed congruency effects, we performed several control analyses. First, if incidental word visibility were responsible for the observed congruency effects, one would expect reliable positive correlations between discrimination scores (*d'*) and congruency effects. However, this was not the

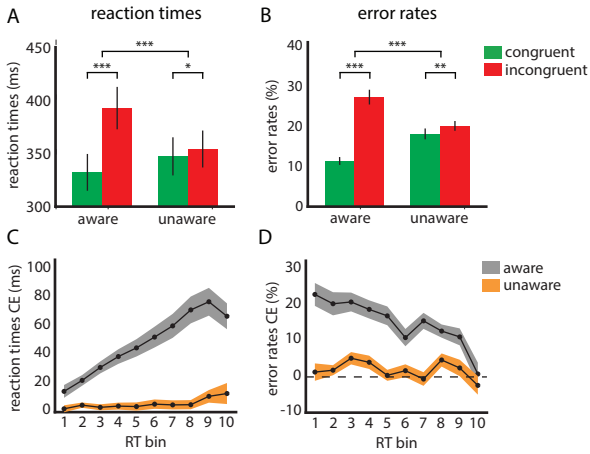

Figure 3.2: Results. (A) Mean RTs (in ms) in the unmasked (aware, left bars) and masked (unaware, right bars) conditions for visual motion stimuli that were preceded by a congruent (green) motion word were faster than when preceded by an incongruent (red) motion word. (B) Mean ERs (%) in the aware condition and unaware condition were lower for congruent than incongruent motion words. (C) The delta plot for reaction times (in ms) congruency effects (incongruent-congruent, CE) in the conscious (grey) condition showed the typical RT conflict-control profile with an initial CE increase over RT bins and a CE decrease in the last bin. In the unaware condition (orange), the CE was not affected by response time and did not decrease in the last bin. (D) Conditional accuracy functions for error rates (%) CE. Stronger response capture is associated with a higher percentage of fast errors. This pattern of decreasing CE across RT bins is present for the aware condition, but not for the unaware condition. Error bars denote SEM. * p<0.05, ** p<0.01, *** p<0.001.

case for RTs (rs=0.17, p=0.34) and ERs (rs=0.19, p=0.28). Further, we used a regression approach, referred to as Greenwald's method (Greenwald et al., 1995) to test whether the reported congruency effects were still significant when discrimination performance was extrapolated to zero visibility (d'=0). Indeed, the linear regression analyses revealed a significant intercept for ERs (intercept=1.73, p=0.018) and a trend for RTs (intercept=5.42, p=0.069) which, although not conclusive, further suggests that congruency effects were induced by masked words that could not be perceived consciously. Next, we split the participants (n=33) into a low visibility (d'<median, n=16) and a high visibility (d'>median, n=17) group. An ANOVA across the masked conditions indicated that there were no significant differences between the congruency effects (CE) between the low and high visibility groups (ERs: low visibility group CE=1.7%; high visibility group CE=2.4%; F1,31=0.29, p=0.59; BF: 1/3.5; RTs: low visibility group CE=3 ms; high visibility group CE=10 ms; F1,31=1.52, p=0.23; BF: 1/2.1). Below, we will describe qualitative differences between the masked and unmasked condition that further suggest that subjects were unable to perceive the masked words (Jacoby, 1991; Merikle et al., 2001).

In summary, both RTs and ERs showed that masked words influenced motion perception, although to a lesser extent than words that were not masked. These results are in line with feed-forward models explaining the effects of language on perception, but not with feedback models.

3.3.3. SPATIAL CHARACTERISTICS OF LANGUAGE-PERCEPTION INTERACTIONS

We reasoned that masked and unmasked words might influence perception in qualitatively different ways, due to the different neural processes involved in both situations (feed-forward vs. recurrent/feedback processing, respectively). First, we tested whether the congruency effect for masked and unmasked conditions was differentially modulated by the visual field in which the visual motion stimuli were presented. For both RTs and ERs, there was no interaction between congruency, awareness and visual field (both *p*s>0.7; RTs: aware: Δ RT LVF: 56 ms, Δ RT RVF: 62 ms; unaware: Δ RT LVF: 5 ms, Δ RT RVF: 8 ms; ERs: aware: Δ ER LVF: 15.5%, Δ ER RVF: 15.7%; unaware: Δ ER LVF: 2.1%, Δ ER RVF: 2.1%). Frequentist statistics provide a measure of confidence in rejecting the null hypothesis, but not a measure of confidence in the null hypothesis itself. In order to verify the true absence of lateralized effects, we calculated Bayes Factors (BF) separately for both masking conditions. We observed moderate evidence (BF <1/3) for the null hypothesis, indicating no effects of visual field on congruency for both masked and unmasked conditions, both in terms of RTs and ERs (aware: RTs: BF=1/4.5; ERs: BF=1/7.2; unaware: RTs: BF=1/6.2; ERs: BF=1/7.4).

3.3.4. TEMPORAL CHARACTERISTICS OF LANGUAGE-PERCEPTION INTERACTIONS

Our previous analyses suggest that language influences perception at higher level conceptual or decision stages (in a feed-forward manner) rather than at low-level sensory stages (in a feedback manner). Therefore, in follow-up analyses, we explored the possible differences in decision and control processes that evolve after the actual integration of perceptual and linguistic information for masked and unmasked conditions. To do so, we calculated so-called 'delta plots', reflecting the RT congruency effects for different RT bins and 'conditional accuracy functions', reflecting the ER congruency effects for different RT bins, to assess the congruency effects across the response time distribution (Forstmann et al., 2008; Jiang et al., 2013; Ridderinkhof, 2002).

The delta plots for the unmasked condition showed the typical RT conflict-control profile (Forstmann et al., 2008; Jiang et al., 2013; Ridderinkhof, 2002). The congruency effects first increased over response time (congruency x RT bin: $F_{1,32}$=24.47, p<0.001) and later decreased in the last bin (2nd-1st vs. 10th-9th bin: T_{32}=2.35, p=0.025; see Figure 3.2C). There was a significant difference between the congruency effects for masked and unmasked conditions over response time (congruency x awareness x RT bin: $F_{1,32}$=13.08, p<0.001) driven by the overall increase in the congruency effect for unmasked but not for masked words. Interestingly, for masked words, the congruency effect was not affected by response time (congruency x RT bin: $F_{1,32}$=1.39, p=0.19) and the RT delta plot did not show the typical control-related decrease in the congruency effect for the last RT bin (2nd-1st vs. 10th-9th bin: T_{32}=-0.06, p=0.955; difference between aware and unaware conditions: T_{32}=1.47, p=0.15). Thus, for the unmasked condition, we found a quick increase in the RT congruency effect with response time, followed by a later decrease, probably as a consequence of the activation of interference control mechanisms. In the masked condition however, RT congruency effects were stable over RT bins and did not show any of the control-dynamics as observed in the unmasked condition.

The strength of automatic response activation by the motion words is inferred from the

pattern of errors present at the shortest RT bins. Stronger response capture is associated with a higher percentage of fast errors (Ridderinkhof, 2002). Again, for accuracy there was a significant three-way interaction (congruency x awareness x RT bin: $F_{1,32}$=3.54, p<0.001), indicating differential effects of response time on congruency for the unmasked and masked conditions. For the unmasked condition, the congruency effect decreased over response time (congruency x RT bin: $F_{1,32}$=7.59, p<0.001), thus showing the typical pattern of these conditional accuracy functions. In contrast, the masked condition showed no modulation over RT bins (congruency x RT bin: $F_{1,32}$=1.35, p=0.22; see Figure 3.2D). Thus, only for the unmasked words a large ER congruency effect was present for the fast RT bins, which is in line with the fact that voluntary control mechanisms take time to be initiated. In the masked condition however, the data pattern was very different and again, like for RT, did not show any of these control-dynamics. Note that this last set of analyses also further suggests that the masked words were invisible. We observed qualitative differences in the effects of masked vs. unmasked motion words on voluntary control mechanisms, but similar effects on congruency effects (reflecting language-perception interactions). These qualitative differences are generally considered as convincing evidence for unconscious perception (Jacoby, 1991; Merikle et al., 2001).

In sum, when the word and the motion stimulus were congruent, both unmasked and masked words sped up motion discrimination and increased discrimination performance compared to incongruent word-motion pairs. Language-perception interactions were equally present for visual stimuli presented in the left and right hemifield, but only in the unmasked condition were voluntary control mechanisms activated across response time to reduce linguistic interference.

3.4. DISCUSSION

We investigated whether language affects perception in a feed-forward or a feedback manner by disrupting the processing of motion words by means of backward masking. The rationale behind this experimental design is that feedback processing is disrupted by masking, as revealed by empirical evidence from monkey electrophysiology and human neuroimaging studies (Del Cul et al., 2007; Fahrenfort et al., 2007; Lamme and Roelfsema, 2000; Lamme et al., 2002). Hence, the feedback model predicts that interactions between language and perception will be abolished under masked conditions. Since backward masking does not affect feed-forward processing, the feed-forward model predicts that effects of language on perception will still be present when the words are masked. Our results support the feed-forward model: When motion words were masked, motion words that were congruent with the direction of the visual motion stimulus resulted in faster and more accurate visual motion direction discrimination relative to incongruent conditions. Thus, our results suggest that language changes perception at a higher, conceptual level, rather than at the lower, sensory level. With several control analyses we verified that our results are unlikely driven by residual visibility of the masked motion words.

A number of previous studies are in line with this interpretation. We recently found that congruent word-motion pairs elicit higher BOLD activity than incongruent combinations in the left middle temporal gyrus (lMTG) (Francken et al., 2015a), an area involved in both lexical retrieval and semantic integration (Hagoort et al., 2009; Menenti et al., 2011). Crucially, there were no effects in motion-sensitive visual areas such as hMT+/V5.

Interestingly, support for this effect was also found by an fMRI study in which linguistic material was only implicitly included. Tan and colleagues had participants judge whether two colored squares had the same or a different color (Tan et al., 2008). Even though the linguistic color vocabulary was irrelevant for the perceptual discrimination task, left temporo-parietal circuits associated with word-finding processes were activated more strongly when subjects had to discriminate between hard-to-name colors compared to easy-to-name colors. These studies indicate that the interaction between language and perception is mediated by 'language areas' that integrate linguistic and visual information. These data stand in sharp contrast to previous proposals that linguistic material describing motion elicits a 'perceptual simulation' in low-level visual areas similar to actually seeing motion (Saygin et al., 2010).

How does language change perceptual decision making according to the feed-forward model? We reason that visual motion stimuli might be conceptually categorized as reflecting evidence for 'upward' and 'downward' motion directions, since participants are required to make a categorical perceptual decision. This may cause conceptual representations to be automatically activated (Tan et al., 2008; Thierry et al., 2009), even though they are not required for task performance. If the conceptual representation activated by the visual motion stimulus matches the conceptual representation that is activated by the motion word, this then results in more activity in lMTG (Francken et al., 2015a), as well as improved behavioral performance. It is also possible that language-perception interactions take place at an even later decision stage. Taken together, the reason why masked (unaware) words are still able to change perception according to the feed-forward model is that the interaction does not depend on feedback of linguistic information to sensory areas. The only requirement is that the masked words are semantically processed, which does indeed occur despite backward masking (Kouider and Dehaene, 2007; van Gaal and Lamme, 2012). Although we show that feed-forward processing is sufficient for language-perception interactions to occur, our data cannot adjudicate whether larger congruency effects under unmasked conditions are due to additional feedback processing or increased stimulus strength.

Proponents of the feedback model argue that language-perception interactions might be dependent on visual 'mental imagery', which is the conscious, internal generation of images (Kosslyn et al., 2001). This process would require feedback from regions up in the cortical hierarchy together with language areas in order to affect low-level sensory processing. For example, when reading stories describing motion events, participants showed a motion aftereffect illusion, which can be interpreted as evidence for direction-selective motion adaptation in the visual system (Dils and Boroditsky, 2010). Interestingly, individuals differed in how early in the story the effect appeared, and this difference was predicted by the strength of an individual's motion aftereffect following explicit motion imagery. Thus, when imagery is sufficiently vivid, language appears to induce changes in the visual system. However, by showing that masked words can still influence perception, we demonstrate here that mental imagery cannot account for all instances of linguistic modulations of perception.

We further qualified the spatial and temporal characteristics of the language-perception interactions. First of all, we did not observe any lateralization of the reported effects. Interestingly, in our previous study in which words were unattended, but not masked, the

RT effect (but not the ER effect) was lateralized to the RVF (Francken et al., 2015a). Therefore, our findings provide an alternative explanation for the often reported (and debated) observation that language exerts stronger effects for stimuli presented in the RVF (Gilbert et al., 2006; Regier and Kay, 2009; Witzel and Gegenfurtner, 2011). This lateralization is explained by the fact that information from the right visual field would have preferential access to the left-lateralized language system (Gilbert et al., 2006; Klemfuss et al., 2012; Regier and Kay, 2009). Although this is an intuitively appealing idea, our data suggests that this depends on the degree to which the linguistic information is attended: Unattended stimuli might show lateralized effects, whereas attended stimuli might not. Future studies are clearly needed to further explore this hypothesis in more detail.

Finally, we observed that decision and control processes that evolve after the integration of perceptual and linguistic information differed between unmasked and masked conditions. In line with previous studies of response conflict (Ridderinkhof, 2002), we reasoned that to suppress the interference of the task-irrelevant words, inhibitory control mechanisms might be activated with increasing response times. Interestingly, these control dynamics were uniquely observed for unmasked words. Thus, although masked words have the power to change perceptual decisions about motion direction, late voluntary control mechanisms to suppress the irrelevant linguistic information were not activated (Tsushima et al., 2006).

First, this finding provides evidence for the notion that there was a clear qualitative difference in awareness between the masked and unmasked conditions. Second, these results inform recent discussions about the role of consciousness in cognitive control and the potential control processes that can unconscious stimuli might be able to affect or even initiate (Ansorge et al., 2014; Kunde et al., 2012; van Gaal et al., 2012). Previously, it has been shown that masked stimuli that explicitly signal the need for control (e.g., an unconscious stop-signal or an unconscious task-switching cue) can elicit behavioral and neural indices of control behavior (Lau and Passingham, 2007; van Gaal et al., 2010, 2008, 2009). However, it has recently been argued that implicit cues, such as specific task properties that have to be derived from repeated exposure to the trials, might not (Kunde et al., 2012). Because in the present experiment masked words were not explicitly associated with control processes, and are in fact irrelevant to perform the motion discrimination task, this might be a situation in which control processes are dependent on awareness. However, some previous studies using non-verbal material (i.e., arrow stimuli) in typical priming tasks have observed control mechanisms irrespective of conflict awareness (Desender et al., 2013; Francken et al., 2011; van Gaal et al., 2010), although evidence is mixed (Ansorge et al., 2014; Kunde et al., 2012; Kunde, 2003) (for reviews see Ansorge et al. (2014); Kunde et al. (2012)). It might be that with the current set-up initial conflict was too small to initiate further control operations in the masked condition (Kunde et al., 2012). Future studies should be performed to further explore in which situations control operations can be triggered implicitly (and explicitly) and in which situations it cannot, and what factors underlie these differences.

In conclusion, here we have manipulated word awareness in a visual motion discrimination task to explore at what level of processing the influence of language on perception takes place. Specifically, we were able to dissociate feed-forward models from feedback models of language-perception interactions. We observed a clear influence of language

on motion discrimination for both masked (unaware) and unmasked (aware) words. Because feed-forward processing remains intact whereas feedback to low-level sensory areas is disrupted by masking, these results can only be explained by a feed-forward model. Therefore, these findings provide evidence for the hypothesis that language-perception interactions occur at stages beyond low-level sensory regions and are mainly driven by interactions at higher-level conceptual and decision stages.

4

EXPLORING THE AUTOMATICITY OF LANGUAGE-PERCEPTION INTERACTIONS: EFFECTS OF ATTENTION AND AWARENESS

Jolien C. FRANCKEN, Erik L. MEIJS, Peter HAGOORT, Simon VAN GAAL and Floris P. DE LANGE

Previous studies have shown that language can modulate visual perception, by biasing and/or enhancing perceptual performance. However, it is still debated where in the brain visual and linguistic information are integrated, and whether the effects of language on perception are automatic and persist even in the absence of awareness of the linguistic material. Here, we aimed to explore the automaticity of language-perception interactions and the neural loci of these interactions in an fMRI study. Participants engaged in a visual motion discrimination task (upward or downward moving dots). Before each trial, a word prime was briefly presented that implied upward or downward motion (e.g., "rise", "fall"). These word primes strongly influenced behavior: Congruent motion words sped up reaction times and improved performance relative to incongruent motion words. Neural congruency effects were only observed in the left middle temporal gyrus, showing higher activity for congruent compared to incongruent conditions. This suggests that higher-level conceptual areas rather than sensory areas are the locus of language-perception interactions. When motion words were rendered unaware by means of masking, they still affected visual motion perception, suggesting that language-perception interactions may rely on automatic feed-forward integration of perceptual and semantic material in language areas of the brain.

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4.1. INTRODUCTION

VISUAL perception arises by an interaction between bottom-up sensory information and several top-down factors, such as attention and expectations (Summerfield and de Lange, 2014). Language has been suggested to be one such important top-down factor that can directly influence perception (Lupyan, 2012a; Winawer et al., 2007; Regier and Kay, 2009). However, it is still debated where in the brain visual and linguistic information are integrated. One possibility is that linguistic information is processed in language-specific regions and then feeds back to lower-level sensory regions to modulate perceptual information processing(Lupyan, 2012a; Meteyard et al., 2007; Hirschfeld et al., 2011). Alternatively, language might influence perception at a later conceptual or decision stage rather than at the sensory stage (Francken et al., 2015a; Klemfuss et al., 2012).

In a previous study, we investigated the effects of motion language on visual motion detection in a combined behavioral and fMRI study (Francken et al., 2015a). Participants were faster and more accurate when the direction implied by a motion word was congruent with the direction of a visual motion stimulus. We observed a neural counterpart of this behavioral facilitation effect in the left middle temporal gyrus (lMTG), an area involved in lexical retrieval, including word semantics and multisensory processing and integration (Menenti et al., 2011). These results are in line with an interaction of language and perception at a conceptual (semantic) processing stage.

In the current study, we aimed to further explore the automaticity of language-perception interactions and the neural loci of this interaction. First, we were interested in the effects of language on visual perception when motion words are attentively processed. In our previous study, motion word primes were irrelevant and ignored. It is conceivable that attentive processing of linguistic material may be necessary for more robust and widespread language-perceptual interactions (Saygin et al., 2010). Second, we tested whether language-perception interactions are dependent on awareness of the linguistic stimuli, i.e., if language still affects perception when participants are unaware of the motion words, in terms of brain and behavior.

To this end, we asked participants to discriminate moving dot patterns (upward or downward moving dots), which were preceded by congruent or incongruent motion word primes (e.g., "rise", "fall") (see Figure 4.1A). To ensure attention on the linguistic prime stimuli, we added a concurrent semantic categorization task, to maximize processing of language stimuli and to enable the possibility for language-perception interactions (on 10% of the trials). To study the neural effects of awareness on language-perception interactions, we manipulated the awareness level of the motion words by backward masking. We previously found that linguistic primes still affect perception when they were perceptually invisible (Francken et al., 2015c), suggesting that language-perception interactions can occur independent of awareness. In the current fMRI study, we similarly manipulated awareness in order to directly study the neural locus of the congruency effect for aware and unaware language primes.

Finally, we were interested in the potential lateralization of language-perception interactions. Previous studies have indicated that these interactions might be larger, or exclusively present, for visual information processed in the language-dominant left hemisphere (Francken et al., 2015a; Gilbert et al., 2006), although evidence is mixed (Witzel and Gegenfurtner, 2011; Brown et al., 2011; Holmes and Wolff, 2012). Therefore,

we explored whether language primes had a stronger effect when visual stimuli were presented in the right hemifield (i.e., when processed by the left hemisphere).

4.2. MATERIALS AND METHODS

4.2.1. PARTICIPANTS

Twenty-six healthy, right-handed participants with normal or corrected-to-normal vision (21 female, age 22.7 ± 2.9 years) took part in two experimental sessions. All participants were native Dutch speakers and reported having no reading problems. The experimental protocol was approved and all participants gave written informed consent in accordance with the declaration of Helsinki and guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands). Compensation was approx. 50 Euros or course credit.

4.2.2. STIMULI

Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997) within MATLAB (MathWorks, Natick, MA, US), and displayed on a rear-projection screen using an EIKI projector (refresh rate: 60 Hz, resolution: 1024 × 768). Stimuli were presented in white on a light-gray background. The visual random-dot motion (RDM) stimuli consisted of white dots (density: 2.5 dots/deg; speed: 6.0 deg/s) plotted within a circular aperture (radius: 7.5 deg). On every trial, the RDM stimulus was presented on either the left or right side of the screen (8.5 deg horizontal eccentricity from fixation to centre of circular aperture) for 200 ms. In the first frame of the RDM stimulus, a random configuration of dots was presented within the annulus. Subsequently, on every frame a certain percentage of the dots was replotted consistently in one direction (upward or downward) on the next frame (see subsection 4.2.3). Dots moving outside of the annulus and other remaining dots were replotted at a random location within the annulus.

Five verbs describing each direction of motion (in Dutch, here translated to English; upward: *grow, ascend, rise, climb, go up*; downward: *sink, descend, drop, dive, go down*), and ten no motion verbs (*bet, mourn, exchange, glow, film, rest, cost, sweat, wish, relax*) were used in the experiment. Motions words and neutral words were matched for lexical frequency (taken from the CELEX database) and word length (5-8 letters)(both p>0.2). Masks were randomly generated combinations of ten consonant strings. Both words and masks were presented at the center of the screen, using capital letters in a mono-spaced font.

4.2.3. PROCEDURE

Participants performed a motion discrimination task (upward vs. downward motion) on a visual RDM stimulus (see Figure 4.1A). A central fixation cross (width: 0.4 deg) was presented throughout the trial, except when a word, mask or blank screen was presented. Each trial started with a centrally presented forward mask (50 ms) followed by a word (33 ms), which could either be a motion word or a no motion (neutral) word. Presentation of the words was pseudorandom. Awareness of the word was manipulated by presenting either backward masks (2 x 33 ms; unaware condition) or a blank screen (67 ms; aware condition) after word presentation. A short inter-stimulus interval (ISI) of 17 ms was

always present after either of these screens. Next, a visual RDM stimulus was presented (200 ms) in either the left visual field (LVF) or in the right visual field (RVF). Participants had to indicate as quickly and accurately as possible whether the RDM contained upward or downward motion, while maintaining fixation at the central cross. The brief presentation time of the RDM stimulus served to minimize the chance of eye movements to the stimulus, as saccade latencies are in the order of 200 ms (Carpenter, 1988). Participants were instructed to respond as quickly and accurately as possible by pressing a button with either the index or middle finger of the right hand (counterbalanced across participants). The inter-trial interval (ITI) was 2133-4133 ms.

In 10% of the trials the motion discrimination task was followed by an additional semantic categorization task (motion or no motion) on the words. These catch trials were included for two reasons. First, they ensured attention to the words, which enhances processing of the primes in both unmasked and masked conditions (Naccache et al., 2002; Spruyt et al., 2012). Second, catch trials were used to estimate word awareness. Participants were explicitly told that there was a fifty percent chance of either motion or no motion words in the catch trials. Note that no motion words were solely included to test for the visibility of the words.

The experiment consisted of two sessions on separate days within one week. In the first session participants performed a training phase outside of the scanner to familiarize them with the task. Participants first practiced the motion discrimination task in three blocks with fixed coherence levels (80%, 55%, and 30% respectively). In the next three training blocks, participants practiced the discrimination task while the words were presented and the catch task was added. The coherence level of the motion stimuli was individually adapted to performance in the previous blocks. In the second session, participants received one block of training within the scanner (motion coherence level from previous session) and the coherence level after this training block was taken as the starting point for a Bayesian adaptive staircase procedure (Watson and Pelli, 1983). This was done to yield comparable task difficulty and performance for all participants. The threshold for discrimination was defined as the percentage of coherent motion for which the staircase procedure predicted 75% accuracy. During training (except for the final training blocks and the threshold estimation block), we provided participants with trial-by-trial feedback for both the motion task and the catch trial task by means of a green or red fixation cross for correct and incorrect responses, respectively.

The actual experiment consisted of ten blocks of 50 trials (500 trials in total). In the experiment, the coherence level was fixed within a block, but was updated between blocks with the same Bayesian staircase procedure, to accommodate potential practice and fatigue effects over the course of the experiment. Summary feedback (percentage correct) was provided during the break after each block.

We also acquired two additional localizer tasks. In the motion localizer, we presented the same motion stimuli that we used in the main experiment (see subsection 4.2.2). The motion coherence level was fixed to 100% and the duration of a trial was 16 s. There were ten blocks of seven trials each, presented in pseudorandom order. Motion presentation occurred in two directions (upward, downward) and at three different locations of the screen (left, center, right). Each combination of motion location and motion direction was present in every block, and counterbalanced across the trials in that block. The last

trial of a block was always a fixation trial in which only a fixation cross was presented. The subject's task was to press a button when the fixation cross turned from white to dark grey (two or three times during a trial, at random intervals), to help them fixate at the center of the screen. The central motion stimulus had an aperture radius of 9 degrees and a central aperture of 1 degree in which the fixation cross was displayed.

In the language localizer, we presented the same word lists that we used in the main experiment (see subsection 4.2.2), plus additional words from the training set, resulting in 10 different words per category. Subjects were presented with eighteen blocks (14 for the first participant) of five trials. Each trial consisted of 300 ms presentations of 25 words alternating with 300 ms fixation (15 s per trial, central presentation). Within a trial, all words were from the same category (upward, downward, no motion, random letter strings (6-8 consonants) and a fixation condition). The order of trials within a block was pseudorandom, with the exception of the fixation trial, which was always the last trial of a block. Participants were instructed to monitor occasional word repetitions (1-back task, occurring 1-4 times per trial) to make sure that they would attentively read the words. Words were presented in the center of the screen. For both localizer tasks, the inter-trial interval was 1 s.

Three participants were excluded from the analyses for reasons outlined below. Performance of one participant on the motion discrimination task was at chance level, one participant had excessive head movement during scanning (>5 mm) and one participant showed a deviant pattern of language lateralization (right-hemisphere dominance). All analyses were performed on the remaining 23 participants.

BEHAVIORAL ANALYSIS

We calculated congruency effects for reaction times (RT) on correct trials and error rates (ER). On congruent trials, the motion described by the word matched the direction of visual motion, e.g. "rise" was followed by a stimulus with upward moving dots. On incongruent trials, the motion described by the word and the direction of visual motion did not match. Missed trials and trials with RTs that were >3 SD than the individual subject mean RT were excluded from the analyses (in total 2.4%). Each of two behavioral measures was subjected to a repeated measures analysis of variance (rm-ANOVA), including factors Congruency (congruent, incongruent), Awareness (aware, unaware) and Visual Field (LVF, RVF).

To assess the awareness of the words, we calculated accuracy and *d'* in the catch trials. *d'* is an unbiased measure of the discriminability sensitivity of the observer (Macmillan and Creelman, 2005). We used the accuracy in binomial tests to determine for every participant whether performance was above chance (50% correct). *d'* for the unmasked and masked conditions were subsequently compared to each other using paired t-tests and then compared with zero using one-sample t-tests.

FMRI ACQUISITION

Images were acquired on a 3.0 Tesla Skyra MRI system (Siemens, Erlangen, Germany). Whole-brain T2*-weighted gradient-echo echo-planar images (repetition time: 2000 ms, echo time: 30 ms, 29 ascending slices, distance factor: 20%, voxel size: 2x2x2 mm, flip angle: 80 degrees, field of view: 192 mm) were acquired using a 32-channel head coil.

A high-resolution anatomical image was collected using a T1-weighted magnetization prepared rapid gradient-echo sequence (repetition time: 2300 ms, echo time: 3.03 ms, voxel size: 1x1x1 mm).

fMRI DATA ANALYSIS

Analysis was performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm, Wellcome Trust Centre for Neuroimaging, London, UK). The first four volumes of each run were discarded to allow for scanner equilibration. Preprocessing consisted of realignment through rigid-body registration to correct for head motion, slice timing correction to the onset of the first slice, coregistration of the functional and anatomical images, and normalization to a standard T1 template centered in MNI space by using linear and nonlinear parameters and resampling at an isotropic voxel size of 2 mm. Normalized images were smoothed with a Gaussian kernel with a full-width at half-maximum of 8 mm. A high-pass filter (cutoff, 128 s) was applied to remove low-frequency signals, such as scanner drift. The ensuing preprocessed fMRI time series were analyzed on a subject-by-subject basis using an event-related approach in the context of the general linear model.

Regressors for the first-level analysis were obtained by convolving the unit impulse time series for each condition with the canonical hemodynamic response function. We modeled the 24 different conditions of the experiment [motion type (2) x word type (3) x visual field (2) x awareness (2)] separately for each of the two sessions. We did not compare the effects of no motion words with motion words because the former were less frequent and occurred more often in catch trials. Catch trials and resting periods were each modeled as a regressor of no interest, as were head motion parameters (Lund et al., 2005). For the localizers, we used the same procedure. Both localizers used a block design. The motion localizer had seven conditions and block duration of 16 s. The language localizer had five conditions and block duration of 15 s.

STATISTICAL ANALYSIS

We used a priori functional information on the basis of the results from the localizers to constrain our search space (Friston et al., 2006). In particular, we isolated the regions that were involved in semantic language processing (language localizer) and visual motion processing (motion localizer). These corresponded to the left middle temporal gyrus (lMTG, language localizer) and bilateral hMT+/V5 (motion localizer).

Specifically, we obtained the anatomical location of the lMTG by contrasting the three word conditions (up, down, neutral words) with the random consonant letter strings condition (MNI coordinates: [-60,-26,2], voxel threshold of p<0.001 uncorrected at the whole brain level). Likewise we obtained the search volume of the right hMT+/V5 ROI by contrasting visual motion stimulation in the LVF > RVF (MNI coordinates: [46,-72,0]) and combining this with a right hMT+/V5 anatomical template (Anatomy Toolbox SPM8), and we used the same procedure to obtain the left hMT+/V5 ROI (with the reverse contrast; MNI coordinates: [-42,-86,8]). We computed the mean activity over the voxels in each ROI for the different conditions and performed an rm-ANOVA, including factors Congruency (congruent, incongruent), Awareness (aware, unaware) and Visual Field (LVF, RVF). Additional whole-brain statistical inference was performed using a cluster-level statistical test to assess clusters of significant activation (Friston et al., 1996). We used

a corrected cluster threshold of $p<0.05$, on the basis of an auxiliary voxel threshold of $p<0.001$ at the whole-brain level.

4.3. RESULTS

4.3.1. BEHAVIORAL RESULTS

In the semantic categorization (catch) task, discrimination performance of the masked words was at chance-level (binominal test, $p>0.05$) for all participants. The discriminability of the words (motion vs. no motion) was markedly lower when the words were masked (unaware condition) than when they were not masked (aware condition) (difference $T_{22}=9.31$, $p<0.001$; unaware $d'=0.00$, corresponding to 49.7% correct responses, $T_{22}=0.02$, $p=0.99$; aware $d'=2.20$, 85.1% correct, $T_{22}=8.75$, $p<0.001$). Thus, the masking procedure yielded clearly distinct aware and unaware conditions.

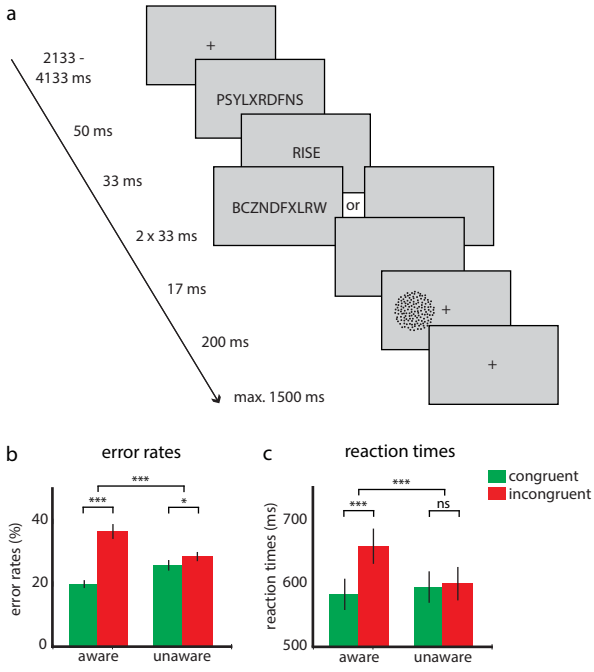


Figure 4.1: Experimental design and behavioral results. (A) A congruent or incongruent motion word (upward or downward, e.g., "rise", or "fall") is displayed in advance of every motion discrimination trial. All words are preceded by a forward mask; unaware words are additionally followed by two backward masks. The visual motion stimulus is presented either in the left or right lower visual field and the dots move upward or downward. In 10% of the trials the motion discrimination task was followed by an additional semantic categorization task (motion or no motion) on the words. (B) Mean error rates (%) in the unmasked (aware, left bars) and masked (unaware, right bars) conditions for congruent (green) word-motion pairs were faster than incongruent (red) word-motion pairs. (C) Mean reaction times (in ms) in the aware condition, but not the unaware condition, were lower for congruent than incongruent motion words. n = 23, error bars denote SEM. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns: not significant.

In the motion discrimination task, participants answered 72.1% of trials correctly

(± 5.8%, mean ± SD) at an average motion coherence level of 48.7% (± 17.7%, mean ± SD). Participants made fewer errors in discriminating the motion stimuli when they were preceded by a congruent motion word than by an incongruent motion word (main effect of congruency: $F_{1,22}$=31.32, p<0.001). This congruency effect was modulated by word awareness (congruency x awareness: $F_{1,22}$=25.52, p<0.001), indicating that the difference between congruent and incongruent conditions was larger when the words were unmasked than when they were masked. The congruency effect was clearly present when the words were unmasked (congruent: ER=20.0%; incongruent: ER=36.8%; ΔER=16.8%, $F_{1,22}$=32.18, p<0.001; see Figure 4.1B), but crucially, it was also present when the words were masked (congruent: ER=26.0%; incongruent: ER=28.8%; ΔER=2.8%, $F_{1,22}$=5.68, p=0.026).

Congruency effects in reaction times showed a similar pattern. Participants responded faster to congruent compared to incongruent trials (main effect of congruency: $F_{1,22}$=53.53, p<0.001). The congruency effect was larger for unmasked words than for masked words (congruency x awareness: $F_{1,22}$=57.91, p<0.001) and was only significant for the unmasked trials (aware: congruent: 584 ms; incongruent: 661 ms; ΔRT=77 ms, $F_{1,22}$=82.22, p<0.001; unaware: congruent: 595 ms; incongruent: 601 ms; ΔRT=6 ms, $F_{1,22}$=0.66, p=0.43; see Figure 4.1C).

In addition, we tested whether the congruency effect for masked and unmasked conditions was differentially modulated by the visual field in which the visual motion stimuli were presented. For both RTs and ERs, there was no interaction between congruency, awareness and visual field (both ps>0.3; ERs: aware: ΔER LVF: 18.4%, ΔER RVF: 16.4%; unaware: ΔER LVF: 2.9%, ΔER RVF: 1.9%; RTs: aware: ΔRT LVF: 73 ms, ΔRT RVF: 85 ms; unaware: ΔRT LVF: 12 ms, ΔRT RVF: -1 ms). In sum, both masked and unmasked words affected visual motion discrimination, although the effects were stronger for unmasked words.

fMRI RESULTS

We next examined the neural locus of the behaviorally observed interaction between language and perception. We a priori identified two ROIs in the visual areas (l/r hMT+/V5) and one in the 'language' areas (lMTG) as possible loci of this interaction (see section 4.2). Only in lMTG an effect of motion words on visual motion perception was observed (MNI coordinates peak voxel: [-60,-32,-2]). In this region, we observed a significant increase in activation for the congruent compared to the incongruent condition for the unmasked condition (See Figure 4.2A,B, $F_{1,22}$=8.80, p=0.007). This congruency effect was significantly larger for the unmasked than for the masked conditions (congruency x awareness: $F_{1,22}$=4.63, p=0.043), and in the unaware condition no such effect was found (congruency: $F_{1,22}$=0.53, p=0.47). The size of the congruency effect for unmasked or masked conditions was not different for LVF compared to RVF stimuli (congruency x awareness x visual field: $F_{1,22}$=1.46, p=0.24).

The left and right visual motion areas both showed a main effect of visual field (lhMT+/V5: $F_{1,22}$=29.19, p<0.001; rhMT+/V5: $F_{1,22}$=7.55, p=0.012), but in contrast to lMTG, no congruency effects were observed for either unmasked or masked conditions (lhMT+/V5: main effect of congruency: $F_{1,22}$=0.07, p=0.79; congruency x awareness: $F_{1,22}$=0.51, p=0.48; rhMT+/V5: main effect of congruency: $F_{1,22}$=0.11, p=0.75; congruency

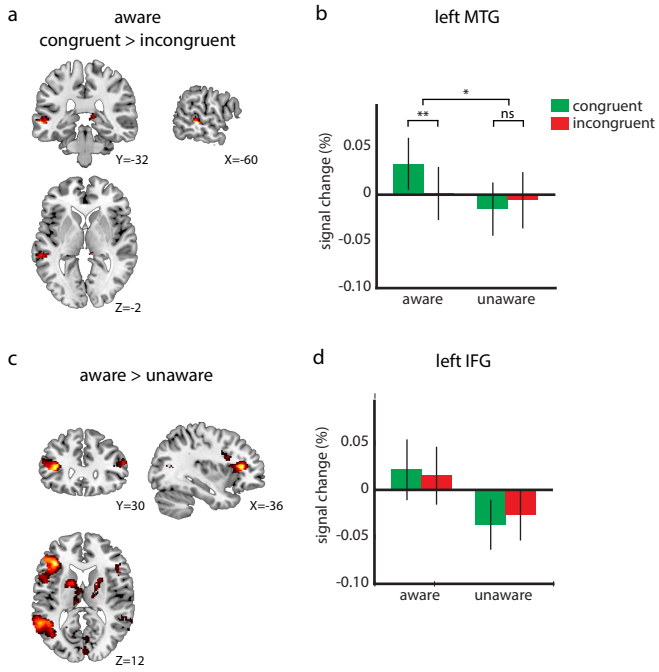


Figure 4.2: fMRI results. (A) The contrast between congruent and incongruent conditions plotted on frontal, sagittal, and transversal slices of an MNI brain (p<0.01 uncorrected for illustration purposes). The only significant modulation because of congruency is localized in lMTG (n = 23). (B) Within the lMTG ROI (based on the independent language localizer) the percentage signal change for the congruent (green) and incongruent (red) conditions is plotted for both the aware (left) and unaware (right) conditions. Only the aware condition shows a congruency effect. (C) The contrast between aware and unaware conditions shows significantly more activation in the lMTG and lIFG for the aware condition (p<0.01 uncorrected for illustration purposes). (D) Within the lIFG region from the contrast between aware and unaware conditions, the percentage signal change for the congruent and incongruent conditions is plotted. There is no modulation of congruency for either the aware or the unaware condition.

x awareness: $F_{1,22}$=0.00, p=1.00). In addition, we were interested in potential differences between unmasked and masked conditions. This whole-brain contrast (corrected for multiple comparisons, see section 4.2) revealed stronger activation in two brain areas: the left inferior frontal gyrus (lIFG, MNI coordinates: [-36,30,12], T_{22}=5.99, p<0.001) and in the left middle temporal gyrus (lMTG, MNI coordinates: [-56,-40,8], T_{22}=5.16, p<0.001) that was previously identified by the language localizer (See Figure 4.2C). A post-hoc ROI analysis revealed that the lIFG was not sensitive to the congruency between the motion word and the visual motion stimulus (main effect of congruency: $F_{1,22}$=0.05, p=0.83; congruency x awareness: $F_{1,22}$=0.57, p=0.46; see Figure 4.2D). Finally, in a whole-brain analysis we confirmed that the congruency effect was specific to the lMTG, since no other regions showed a congruency effect under either unmasked or masked conditions.

Together, the fMRI data show that only the lMTG is sensitive to the difference between congruent and incongruent motion words in a visual motion perception task, showing a stronger response when language primes and visual motion signals correspond. These

effects were only observed when motion words were consciously perceived.

4.4. DISCUSSION

WE investigated the dependence of language-perception interactions on motion word awareness and the neural loci of this interaction. In a visual motion discrimination task in which attention was explicitly directed to motion word primes, congruent motion words significantly sped up reaction times and improved performance relative to incongruent motion words. Despite the large behavioral effects, language-perception congruence affected only the lMTG, where neural activation was higher for congruent compared to incongruent conditions. This neural congruency effect was obliterated by masking the words, even though a small behavioral effect persisted.

In a previous study, we investigated behavioral and neural effects of motion words on visual motion detection (Francken et al., 2015a). When comparing those results to our current findings, we notice that the behavioral congruency effects in the current study were much stronger: In the previous study, the difference between congruent and incongruent conditions was on average 20 ms (RTs) and 4% (ERs), while in the current study the difference was more than three times larger (70 ms and 15%). This difference is easily explained by the fact that the current study included an additional semantic categorization task on the motion words, while in the previous study the words were task-irrelevant and therefore unattended.

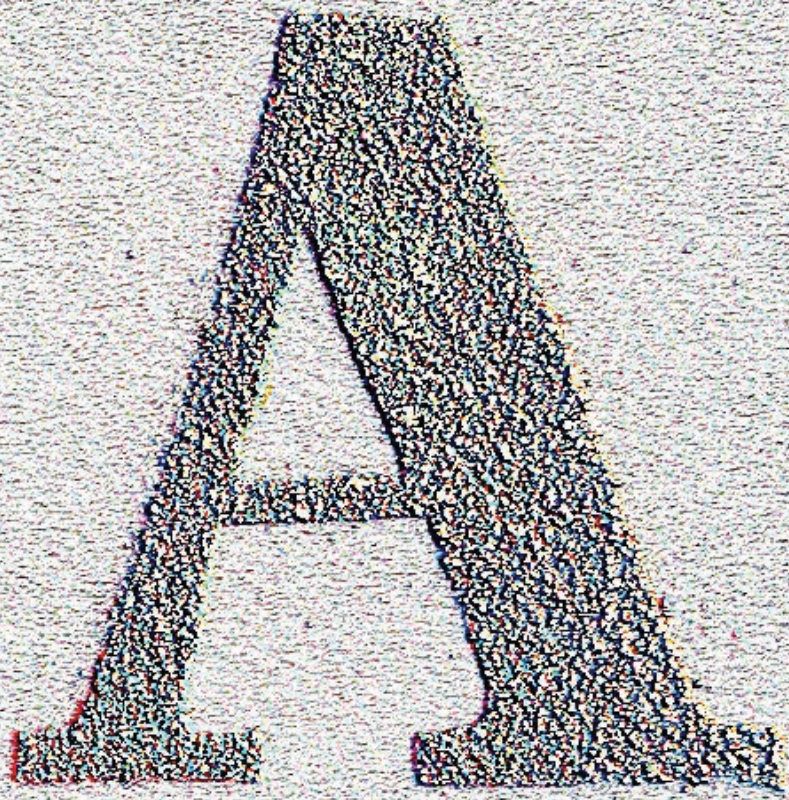
We next examined whether increased attention to the motion words also resulted in an interaction of language primes and visual stimuli in a wider network of brain areas, feeding back to sensory areas. Interestingly however, the only brain region that was sensitive to the difference between congruent and incongruent conditions was the lMTG, replicating our previous results (Francken et al., 2015a). Based on these results we conclude that motion sensitive sensory areas do not seem to be involved in the integration of linguistic and perceptual information, even when both are thoroughly processed, contrary to suggestions from previous studies (Lupyan, 2012a; Saygin et al., 2010). Our findings rather provide evidence for a feed-forward model of language-perception interactions (Francken et al., 2015c). Within this model, motion words and motion signals are each processed in separate areas, which do not interact. Both signals activate a (common) conceptual representation (embodied in the lMTG), however, and it is here at the conceptual level that linguistic information interacts with the visual motion stimuli (Noel et al., 2015). This suggests that semantic categorization may be an integral part of perceptual decision making (Francken et al., 2015a; Tan et al., 2008; Ting Siok et al., 2009).

We further asked whether language-perception interactions can also occur outside of subjects' awareness. In line with a previous study (Francken et al., 2015c), we provide support for this notion by showing larger error rates for invisible motion words that were incongruent with upcoming visual stimuli, compared to congruent motion words. We did not observe robust differences in brain activity between congruent and incongruent stimuli when the motion words were unconscious. When comparing neural activity for consciously perceived vs. unconscious motion words, there was larger activity in a left-lateralized language network comprising the lMTG and the lIFG. Within this network, lMTG is implicated in lexical retrieval, including word semantics and multisensory processing and integration (Menenti et al., 2011; Hagoort et al., 2009; Noppeney et al., 2008;

Snijders et al., 2010, 2009; Beauchamp et al., 2004) whereas the lIFG is involved in unification operations that maintain, select, and integrate multiple sources of information over time (Hagoort et al., 2009; Snijders et al., 2009, 2010). Of these two areas, congruence effects were only observed in the lMTG. We speculate that this is due to the fact that the congruence effect happens at the level of the conceptual representation, rather than the level of selection and maintenance of semantic material.

Finally, there has been mixed support for a lateralization of language-perception interactions (Regier and Kay, 2009; Gilbert et al., 2006; Witzel and Gegenfurtner, 2011; Brown et al., 2011; Holmes and Wolff, 2012). In fact, using a highly similar design, we previously observed stronger congruency effects for stimuli presented in the right visual field (Francken et al., 2015a) but equal congruency effects in the current study and a previous behavioral study (Francken et al., 2015c). A critical difference between these studies is the extent to which attention was paid to the language primes. We speculate therefore that lateralization of language-perception interactions may depend on the extent to which attention is directed to the language stimuli. Unattended stimuli may 'remain local' and thereby only affect visual processing in the same hemisphere leading to unilateral effects, whereas attended stimuli might be 'broadcasted' to other neural processors (Dehaene et al., 2003; Dehaene and Naccache, 2001), resulting in larger and bilateral effects. Future studies are required to directly assess the potential effects of attention on language-perception interactions.

In conclusion, we have explored the neural locus and behavioral characteristics of language-perception interactions for attended motion words, under different conditions of awareness. Motion words had large behavioral effects on visual perception. A neural counterpart of this integration process was observed in the lMTG, suggesting that higher-level conceptual areas, rather than sensory areas, are the locus of language-perception interactions.



5

ANIMALS VERSUS ELEPHANTS: THE EFFECTS OF CONCEPT HIERARCHY AND TYPICALITY ON LANGUAGE-PERCEPTION INTERACTIONS

Jolien C. FRANCKEN, Floris P. DE LANGE and Peter HAGOORT

How does language modulate perception? Previous studies have suggested two possible mechanisms that may underlie language-perception interactions. First, language might act as a top-down factor on sensory representations, similar to the top-down effects of attention or expectation. Alternatively, sensory input is automatically semantically categorized and subsequently interacts with other conceptual representations within the language network. Here, we investigated whether the locus of language-perception interactions depends on the specificity of linguistic information in a behavioral and an fMRI experiment. We presented cues at the category (e.g., "animal") and exemplar (e.g., "elephant") level of the conceptual hierarchy followed by congruent or incongruent picture targets that had to be semantically categorized. In addition, we varied the typicality of the target pictures to test whether category cues interact differently with a typical category member compared with an atypical category member. We found that both category and exemplar cues sped up reaction times to congruent relative to incongruent targets. The left middle temporal gyrus, an area involved in semantic processing, was found as the neural counterpart of this congruency effect. In addition, incongruent exemplar cues elicited higher activation in the left early visual cortex relative to congruent conditions, providing some evidence for the hypothesis that only exemplar cues activate a perceptual template. We did not find any behavioral or neural differences between typicality conditions. Our findings might provide a possible solution to the debate on the locus of effects of language on perception by suggesting that the mechanism might differ depending on the specificity of linguistic information.

5.1. INTRODUCTION

PERCEPTION involves the categorization of sensory input into concepts. For instance, we are only able to detect visual objects in natural environments if we recognize what is part of the object and what is its background. Furthermore, conceptual categorization enables us to abstract away from irrelevant differences in sensory input. A golden retriever and a dachshund are both dogs, but they would not be categorized into the same conceptual category on the basis of perceptual features only. Categorization is enabled by the use of language, and more specifically, words, to refer to things in the outside world. An important question is whether words merely label our existing concepts or whether they are in turn also able to change the concepts and percepts they refer to (Lupyan, 2012b). Previous studies indeed observed influences of language on perception and cognition. For instance, color perception is shaped by the color terminology of one's language (Winawer et al., 2007) and motion detection performance is facilitated by concurrent presentation of task-irrelevant congruent motion words (Francken et al., 2015a; Meteyard et al., 2007).

But how does language change the way we categorize or see the world? Previous studies have suggested two possible mechanisms that may underlie language-perception interactions. The first possibility is that language might act as a top-down factor on sensory representations, similar to the top-down effects of attention or expectation (Summerfield and de Lange, 2014). According to this feedback model, when a linguistic stimulus, e.g., the word "elephant", is heard or read, feedback activity from the language areas in the brain activates visual areas to prepare for the sensory processing of the expected visual input of an elephant (Lupyan, 2012a). Alternatively, according to the feed-forward model of language-perception interactions, sensory input is automatically semantically categorized and subsequently interacts with other conceptual representations within the language network (Francken et al., 2015a,c). Thus, upon seeing an elephant, the sensory information is conceptually categorized as "elephant" and subsequently this semantic representation interacts with the activated concept after hearing or reading the word "elephant".

Neural effects of language-perception interactions have been observed in sensory areas (Dikker and Pylkkanen, 2011, 2013; Hirschfeld et al., 2011; Thierry et al., 2009), providing evidence for the feedback model. Evidence for the feed-forward model has been provided directly by a couple of neuroimaging studies, showing automatic activation of areas in the language network of the brain (e.g., the left middle temporal gyrus (lMTG)) in a (non-verbal) color discrimination task (Tan et al., 2008; Ting Siok et al., 2009) and effects in the same location when comparing congruent motion word and visual motion stimuli to incongruent word-motion pairs (Francken et al., 2015a,b). Thus, it is currently unclear whether language affects perception at a sensory or rather at a later conceptual stage.

Here, we investigated the possibility that both models are valid, however each under different circumstances. We hypothesized that concept hierarchy might affect the locus of the interaction. For instance, when encountering a category cue such as "animal", it is not possible to activate a specific perceptual template in the sensory areas, because it is uncertain which animal will appear. On the other hand, when cued with a concept at a lower or more specific level of the conceptual hierarchy, e.g., "elephant", the effect on perception might arise from an interaction in sensory areas (Puri and Wojciulik, 2008).

An alternative hypothesis with respect to the category cues follows from the 'prototype theory' (Mervis and Rosch, 1981; Rosch, 1973). According to this theory, category cues also activate a perceptual template, namely one of the most (proto)typical items of the category (e.g., a dog or cat after the word "animal"). Thus, language-perception effects of higher- or category-level concepts might also result in interactions in sensory areas, but only for typical items. Another possibility is that neither higher- nor lower-level concepts interact with visual stimuli at a sensory stage, but rather both affect perception at a later conceptual stage, in line with previous evidence for the feed-forward model of language-perception interactions (Francken et al., 2015a,c).

Thus, we propose that the conflicting findings in the literature might result from the fact that the locus of the interaction depends on whether the cue activates a specific perceptual template. To test this hypothesis, we performed a behavioral and an fMRI experiment in which we presented participants single word cues paired with congruent or incongruent picture targets that had to be semantically categorized. To investigate whether the interaction between language and perception is affected by cue specificity, the words provided information at either the category level ("animal", "tool") or at the exemplar level (e.g., "elephant"). In addition, we included cue-only conditions in which no target picture was presented to assess whether and where category and exemplar cues activate a perceptual template independent of interactions with visual stimuli. Finally, to test whether category cues activate a perceptual template of a typical category member compared with an atypical category member, we varied the typicality of the target pictures.

5.2. MATERIALS AND METHODS

5.2.1. PARTICIPANTS

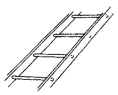
The experiment consisted of a behavioral and a neuroimaging (fMRI) part. Thirty participants (8 males, 22 females; age range: 19-38 years) were included in the behavioral study and twenty-five (6 males, 19 females; age range: 18-29 years) participants engaged in the fMRI study. All participants were right-handed, had normal or corrected-to-normal vision, were native Dutch speakers and had no reading problems. Compensation was 12 Euros for participation in the behavioral study and 25 euro for participation in the fMRI study. All participants gave written informed consent, in accordance with the declaration of Helsinki and guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands). One participant was excluded from the fMRI study because of excessive head movement during scanning (>5 mm).

5.2.2. STIMULI

Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997) within MATLAB (MathWorks, Natick, MA, US), and displayed on a BENQ XL2420T monitor in the behavioral experiment and on a rear-projection screen using an EIKI projector (refresh rate: 60 Hz, resolution: 1024×768) in the fMRI experiment. Stimuli were presented in black and white on a light-gray background. Six exemplar animal/tool names and two category names (see Table 5.1) were used in the experiment. Exemplars were selected on the basis of typicality estimates obtained in a pre-test (n=17). Animal and tool exemplar names had comparable mean lexical frequency (taken from the CELEX database) and

word length. Words were presented at the centre of the screen, using capital letters in a mono-spaced font. On each regular trial, one out of six different pictures from the Snodgrass and Vanderwart dataset (Snodgrass and Vanderwart, 1980) was centrally presented (max. width/height 3 deg; see Table 5.1).

Table 5.1: Experimental stimuli. Six different Dutch exemplar cues and two category cues were used (English translation between brackets). The exemplar cues corresponded to six different target pictures of three animals and three tools, varying in typicality ratings from typical, to medium typical, and atypical.

examplar cues	target	typicality
olifant (elephant)		typical
hert (deer)		medium typical
kreeft (lobster)		atypical
hamer (hammer)		typical
schaar (scissors)		medium typical
ladder (ladder)		atypical
category cues		
dier (animal)		
gereedschap (tool)		

5.2.3. PROCEDURE

Participants performed a semantic categorization task (animal or tool category) on the visually presented target picture (see Figure 5.1). A central fixation cross (width: 0.4 deg)

was presented throughout the trial, except when the word or picture was presented. Each trial started with a centrally presented word (0.5 s), which could either be a category name or an exemplar name. In regular trials, after an inter-stimulus interval (ISI) of 0.5 s a target picture was presented for 1 s. There were six possible pictures (three animals and three tools), and the probability of seeing the target picture described by the cue was therefore 1/6 for the exemplar cues and 1/2 for the category cues, since every picture occurred equally often.

Participants had to indicate whether the picture depicted an animal or a tool, while maintaining fixation at the central cross. In cue-only trials (20% of the trials), after the presentation of the word no picture was presented. In this case, participants had to indicate whether the cue referred to an animal or a tool. Participants were instructed to respond as quickly and accurately as possible by pressing a button with either the index or middle finger of the right hand (counterbalanced across participants). The inter-trial interval (ITI) was 2200-2217 ms in the behavioral experiment and 4000-6000 ms in the fMRI experiment.

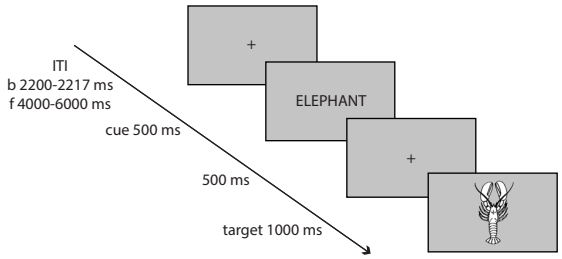


Figure 5.1: Experimental design. A congruent or incongruent category or exemplar cue is displayed before every target picture presentation. In this example, an incongruent (within-category) exemplar condition is shown. ITI = inter-trial interval, b = behavioral experiment, f = fMRI experiment.

Participants first performed a training phase to familiarize them with the task. In the behavioral experiment, in the first block (20 trials) trial-by-trial feedback was provided by means of a green or red fixation cross for correct and incorrect or missed responses, respectively. In the second block (36 trials) and the actual experimental blocks, summary feedback (percentage correct) was provided after each block. In the fMRI experiment, the training consisted of one block (56 trials) with trial-by-trial feedback. The actual behavioral experiment consisted of ten blocks of 112 trials (1120 trials in total), while in the fMRI experiment ten blocks of 60 trials were presented (600 trials in total) in pseudorandom (counterbalanced) order.

In the fMRI experiment, we also acquired a localizer task in which we presented the same pictures that we used in the main experiment (see subsection 5.2.2). The duration of a trial was 1 s with an ITI of 4-6 s. There were two blocks of 56 trials each, presented in pseudorandom (counterbalanced) order. The subject's task was to press a button when a target picture (a picture of a leaf from the same dataset) was presented, to help them fixate at the center of the screen.

5.2.4. BEHAVIORAL ANALYSIS

We calculated congruency effects for reaction times (RT) on cue-target trials with correct responses. On congruent trials, the item described by the word matched the picture object, e.g., "elephant" or "animal" was followed by a picture of an elephant. On incongruent trials, the item described by the word and the actual object in the picture did not match. Within the exemplar cue conditions, two types of incongruency can be distinguished: Within-category incongruency (exemplar cue incongruent within-category (EC-IW), e.g., "elephant" + lobster) and between-category incongruency (exemplar cue incongruent between-category (EC-IB), e.g., "hammer" + lobster). Typicality effects were calculated only for category cue conditions. Missed trials and trials with RTs that were <200 ms or >3 SD than the individual subject mean RT were excluded from the analyses (in total 2.8%).

To assess whether the cues affected target categorization, we used paired t-tests (two-tailed) to compare RTs between congruent and incongruent, congruent and EC-IW, and EC-IW and EC-IB conditions for the exemplar cues, and congruent and incongruent conditions for the category cues. We also checked whether congruency effects were different for animal and tool targets by means of a repeated measures analysis of variance (rm-ANOVA) including the factors Target category (animal, tool) and Congruency (congruent, incongruent). To test whether the effects differed between the experiments, we included the between-subjects factor Experiment (behavioral, fMRI). Further, to assess the effect of typicality on RTs, we performed a rm-ANOVA with factors Typicality (typical, medium typical, atypical), Congruency, and Experiment.

5.2.5. FMRI ACQUISITION

Images were acquired on a 1.5 Tesla Avanto MRI system (Siemens, Erlangen, Germany). Whole-brain T2*-weighted gradient-echo echo-planar images (repetition time: 2000 ms, echo time: 40 ms, 28 ascending slices, voxel size: 3.5x3.5x3.5 mm, flip angle: 90 degrees, field of view: 224 mm) were acquired using a 32-channel head coil. A high-resolution anatomical image was collected using a T1-weighted magnetization prepared rapid gradient-echo sequence (repetition time: 2730 ms, echo time: 2.95 ms, voxel size: 1x1x1 mm).

5.2.6. FMRI DATA ANALYSIS

Analysis was performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm, Wellcome Trust Centre for Neuroimaging, London, UK). Since the exact time of the first scan was not correctly saved for 32 of the 48 experimental sessions (24 subjects x 2) and eight of the 24 localizer sessions, we calculated the offset between the scanner PC and the stimulus presentation PC of the correctly saved sessions and used this to obtain an approximation of the time of the first scan for the missing sessions. This procedure was possible due to the fairly constant temporal offset beween the two PCs (SD of difference: 0.48 s). The first four volumes of each run were discarded to allow for scanner equilibration. Preprocessing consisted of realignment through rigid-body registration to correct for head motion, slice timing correction to the onset of the first slice, coregistration of the functional and anatomical images, and normalization to a standard T1 template centered in MNI space by using linear and nonlinear parameters and resampling at an isotropic voxel size of 2 mm. Normalized images were smoothed with a Gaussian kernel with a full-width at

half-maximum of 8 mm. A high-pass filter (cutoff, 128 s) was applied to remove low-frequency signals, such as scanner drift. The ensuing preprocessed fMRI time series were analyzed on a subject-by-subject basis using an event-related approach in the context of the general linear model.

Regressors for the first-level analysis were obtained by convolving the unit impulse time series for each condition with the canonical hemodynamic response function. We modeled 22 different conditions of the experiment (for exemplar cues [cue category (2) x congruency (3)] + for category cues [cue category (2) x congruency (2) x typicality (3)] + for cue-only trials [cue type (2) x cue category (2)]). Text before and after resting periods was modeled as a regressor of no interest, as were head motion parameters and first-order temporal derivatives. For the localizer, we used the same procedure. Catch trials were modeled as a regressor of no interest.

5.2.7. STATISTICAL ANALYSIS

We used a priori functional and anatomical information to constrain our search space (Friston et al., 2006). In particular, we determined the regions that were involved in semantic language processing and visual processing of the pictures. These corresponded to the left middle temporal gyrus (lMTG), bilateral early visual cortex (EVC), and bilateral lateral occipital complex (LOC). Specifically, we obtained search volumes of the l/r LOC ROI by contrasting visual stimulation > baseline in the localizer (MNI coordinates lLOC: [-46, -78, 4], rLOC: [48, -72, -2]) and combining this with a sphere (r=10 mm) around each of the peak coordinates. For the lMTG ROI we also obtained search volumes by taking spheres (r=10 mm) around the peak coordinate ([-58, -36, -6]) from Francken et al. (2015a). Finally, we used the anatomical templates from the Anatomy Toolbox (SPM8) to create search spaces for l/r EVC.

We corrected our results for multiple comparisons using a family-wise error rate threshold of p<0.05 within the search volumes (Worsley, 1996) on the basis of an auxiliary voxel threshold of p<0.001 at the whole-brain level. For additional exploratory whole-brain analyses, statistical inference was performed using a corrected cluster threshold of p<0.05, also on the basis of a threshold of p<0.001 at the voxel level.

5.3. RESULTS

5.3.1. BEHAVIORAL RESULTS

We analyzed the behavioral data from the behavioral experiment and the fMRI experiment within one statistical model that considered experimental session as a factor. Overall, participants indicated whether the target depicted an animal or a tool with low error rate (ER=4.5 ± 3.1%, mean ± SD; cue categorization in cue-only trials: ER=8.9 ± 7.1%, mean ± SD).

First, we looked at the effects of exemplar cues on categorization. Congruent relative to incongruent exemplar cues resulted in faster semantic categorization of the target pictures (congruent: RT=609 ms; incongruent: RT=640 ms; ΔRT=31 ms; T_{53}=11.38, p<0.001; see Figure 5.2A). However, this congruency effect may be driven by incongruent between-category conditions (EC-IB, e.g., "hammer" + lobster), rather than incongruent within-category conditions (EC-IW, e.g., "elephant" + lobster), reflecting a category effect rather

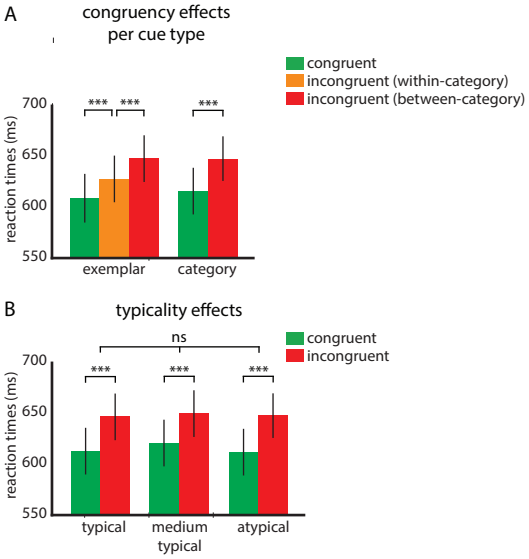


Figure 5.2: Behavioral results. A. Mean RTs (in ms) for target pictures that were preceded by exemplar cues (left bars) or category cues (right bars). Exemplar cues could be congruent (green), incongruent from the same category (EC-IW; orange), or incongruent and from the other category (EC-IB; red) with respect to the target. Category cues were either congruent (green) or incongruent (red) with the target. B. Mean RTs (in ms) for congruent (green) and incongruent (red) cue-target pairs. Target pictures varied in typicality from typical, to medium typical, to atypical (x-axis). n = 54, error bars denote SEM. *** p<0.001, ns not significant.

than an exemplar effect (Puri and Wojciulik, 2008). Therefore, we tested whether the congruent condition was responded to faster than the EC-IW condition, which was indeed the case (EC-IW: RT=628 ms; ΔRT=19 ms; T_{53}=7.34, p<0.001). In addition, EC-IW conditions resulted in faster RTs than EC-IB conditions (EC-IB: RT=648 ms; ΔRT=20 ms; T_{53}=6.04, p<0.001), indicating a relative benefit from incongruent cues that have a closer semantic relation with targets (EC-IW), i.e., when they refer to the same category.

Second, we tested whether category cues also affected semantic categorization of the target pictures. Indeed, congruent category cues sped up RTs relative to incongruent category cues (congruent: RT=616 ms; incongruent: RT=648 ms; ΔRT=32 ms; T_{53}=6.72, p<0.001). There was no interaction of any of the reported effects with the factor experiment (all p>0.2).

Third, although our experiment was not designed to look at differences between animal and tool targets, we tested whether congruency effects were different for animal or tool pictures. Congruency effects for animal and tool targets were similar (target category x congruency: $F_{1,52}$=0.66, p=0.42; animal target CE=36 ms; tool target CE=30 ms; target category x congruency x experiment: $F_{1,52}$=1.82, p=0.18).

To test whether category cues activate a typical target more than an atypical target, we sorted the targets by typicality. There was no RT advantage for typical compared to medium typical and atypical targets ($F_{2,104}$=1.19, p=0.31). Also no differences in congruency effects between typical, medium typical and atypical conditions were observed

($F_{2,104}$=0.55, p=0.58; see Figure 5.2B). There was no interaction of any of these effects with the factor experiment (all p>0.2).

In summary, congruent exemplar cues sped up RTs to target pictures relative to both incongruent within- and between-category exemplar cue conditions. Category cues showed a congruency effect as well. Our typicality manipulation did not result in RT differences between the typicality conditions (typical, medium typical, and atypical).

5.3.2. fMRI RESULTS

Since we were interested in the interaction between semantic language processing and visual processing of the target pictures, we restricted our fMRI analyses to three different neural processing stages: The early visual processing stage (bilateral early visual cortex (l/r EVC)), the object-selective visual processing stage (bilateral lateral occipital complex (l/r LOC)), and the semantic processing stage (left middle temporal gyrus (lMTG)).

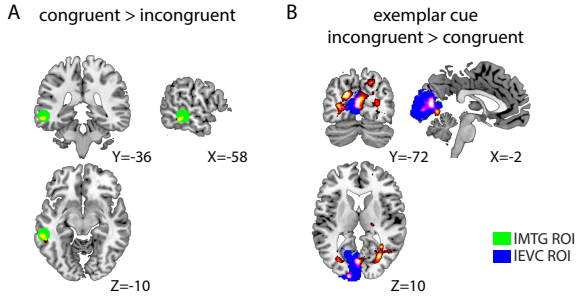


Figure 5.3: fMRI results. A. Activation for congruent > incongruent conditions plotted on frontal, sagittal, and transversal slices of an MNI brain (p<0.01 uncorrected for illustration purposes). The region in green corresponds to the lMTG ROI. B. Activation for incongruent > congruent exemplar cue conditions. The area in blue corresponds to the lEVC ROI. Other conventions as in A. n = 24.

First, to test whether and where semantic cues impact on categorization of the target pictures, we looked at congruency effects of cue-target pairs. Only in the lMTG there was a trend of higher activation for congruent conditions relative to incongruent conditions (T_{23}=3.51, p=0.056; see Figure 5.3A), confirming our earlier reports of larger activity in this area for congruent semantic and visual information (Francken et al., 2015a,b). An exploratory whole-brain analysis outside of our ROIs furthermore revealed a trend for higher activation of incongruent conditions than congruent conditions in the right parietal cortex (MNI coordinates: [30, -34, 60], T_{23}=4.87, p=0.058). To test whether congruency effects for animal targets were selective to the ventral stream and those of tool targets to the dorsal stream, we examined the interaction between congruency and target category. No such effects were present, however in the left and right prefrontal cortex (l/rPFC) we did observe higher activation for animal target congruency (congruent > incongruent) relative to tool target congruency (MNI coordinates lPFC: [-38, 42, 4], T_{23}=4.97, p<0.001; MNI coordinates rPFC: [24, 50, 24], T_{23}=4.77, p=0.031; see Figure 5.4).

Second, we examined the congruency effects for the cue types separately. Incongruent exemplar cues elicited marginally significantly more activation in lEVC than congruent exemplar cues (T_{23}=3.91, p=0.054; see Figure 5.3B). No congruency effects were found in

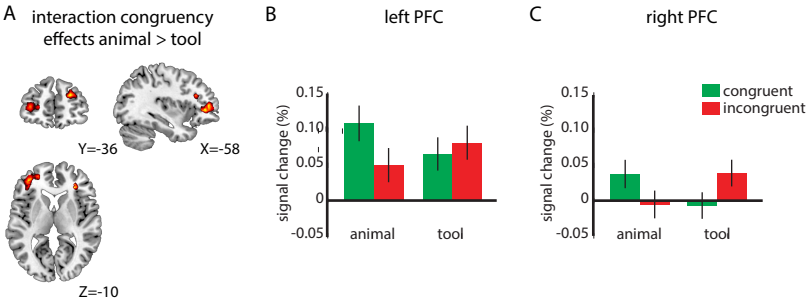


Figure 5.4: Supplementary figure. Congruency effects for animal and tool target conditions. A. Activation for animal target conditions congruent > incongruent larger than tool target conditions congruent > incongruent. Conditions plotted on frontal, sagittal, and transversal slices of an MNI brain (p<0.001 uncorrected for illustration purposes). B. Within the activated part of lPFC, the percentage signal change for the congruent (green) and incongruent (red) conditions is plotted for both animal target (left) and tool target (right) conditions. C. Percentage signal change in rPFC. Other conventions as in B.

5

the other ROIs for exemplar cues (p>0.1 or no suprathreshold voxels). Motivated by the behavioral results, we performed additional analyses to see whether this exemplar cue congruency effect was driven by the EC-IB rather than EC-IW conditions, however for none of the comparisons we found significant neural differences (p>0.2 or no suprathreshold voxels). Next, we compared the congruent and incongruent category cue conditions. Here, none of the ROIs showed a congruency effect for category cues (all ps>0.10).

Third, we tested where the cue-only conditions affected neural activation to directly test our hypothesis that exemplar cues, but not category cues, induce a perceptual template. None of the ROIs was sensitive to the difference between category and exemplar cues in the cue only conditions (no suprathreshold voxels in any of the ROIs). In an additional exploratory whole-brain analysis, left lateral PFC showed higher activation for category cues relative to exemplar cues (MNI coordinates: [-46, 8, 50], T_{23}=5.63, p=0.041).

Finally, congruency effects did not differ between typicality conditions in any of the ROIs, in line with the null results in the behavioral data, which already suggested that our typicality manipulation was unsuccessful.

To sum up, congruent conditions elicited higher neural activation in the lMTG compared to incongruent conditions, while the opposite contrast activated an area in the right parietal cortex. When we examined the congruency effects for exemplar cues and category cues separately, we found that incongruent exemplar cues activated the lEVC more strongly than congruent exemplar cues. When the cues were presented without subsequent targets, we did not observe differences between exemplar and category cues in any of our ROIs, though category cues did activate the lPFC more strongly than exemplar cues.

5.4. DISCUSSION

HOW does language modulate perception? Here, we investigated whether the locus of language-perception interactions depends on the specificity of linguistic information. We showed that cues at different levels of the conceptual hierarchy, i.e., the category

(e.g., "animal") and exemplar (e.g., "elephant") levels, both affect response times to target pictures in a semantic categorization task. A region in the 'language areas' of the brain, the lMTG, was found as the neural counterpart of this congruency effect. In addition, incongruent exemplar cues elicited higher activation in the lEVC relative to incongruent conditions, providing some evidence for the hypothesis that only exemplar cues activate a perceptual template.

Previous studies reported effects of linguistic information on various behavioral and neural measures of visual perception of e.g., color, motion, faces and objects (Eger et al., 2007; Francken et al., 2015a; Landau et al., 2010; Puri and Wojciulik, 2008; Winawer et al., 2007). However, the neural mechanism underlying these language-perception interactions is still debated. In two previous studies investigating the effects of motion language on motion perception (Francken et al., 2015a,b), we observed congruency effects in the lMTG, but no effects in visual areas. In the current study we also found that congruent semantic cues elicited higher neural activation relative to incongruent conditions in the lMTG. This area is part of the 'language network' of the brain, and it is involved in lexical retrieval, including word semantics and multisensory processing and integration (Beauchamp et al., 2004; Hagoort et al., 2009; Menenti et al., 2011; Noppeney et al., 2008). Several other studies also reported neural effects of language on perception in 'language areas' (Sadaghiani et al., 2009; Tan et al., 2008). Together, these studies suggest that interactions between language and low-level visual stimuli (motion, color) as well as language-perception interactions involving the more complex visual stimuli that we used here (objects) occur at a later, semantic processing stage, providing evidence for a feed-forward model of language-perception interactions. According to this model, sensory input is automatically semantically categorized and subsequently interacts with other conceptual representations within the language network (Francken et al., 2015c).

However, there is also empirical evidence for the feedback model, in which linguistic information acts as a top-down factor on sensory representations (Dikker and Pylkkanen, 2011, 2013; Hirschfeld et al., 2011) similar to attention and expectation (Desimone and Duncan, 1995; Summerfield and de Lange, 2014). Interestingly, our results might explain these divergent findings by suggesting that the neural mechanism underlying language-perception interactions depends on the specificity of linguistic information. We hypothesized that lower or more specific levels of the conceptual hierarchy might induce a perceptual template, similar to mental imagery (Kosslyn et al., 2001), as a result of which the effect on perception may arise from an interaction in sensory areas. On the contrary, linguistic information at a higher level of the conceptual hierarchy might not activate a specific perceptual template in the sensory areas, because it is uncertain what perceptual input to expect, and therefore perception is modulated at a later processing stage.

In line with the 'perceptual template' hypothesis, we observed that incongruent relative to congruent exemplar cue conditions elicited higher neural activation in the lEVC. The results from two studies by Dikker and Pylkkanen also support this hypothesis (Dikker and Pylkkanen, 2011, 2013). They used MEG to study the effects of picture primes on visually presented words in a semantic verification task (essentially reversing the order of the events in comparison with our current study). In the congruent condition a picture cue was followed by its accompanying name in 50% of the cases, and by a word with a completely different word form in the remaining trials. These latter incongruent condi-

tions elicited higher amplitudes relative to congruent conditions over bilateral occipital sensors in an early time-window (~100 ms), indicating that the visual word form is predicted at the early sensory level. Furthermore, they found that in a later time-window (250-400 ms, left hemisphere sensors) congruent conditions elicited less activity than incongruent conditions. The authors suggested that the picture cue might have activated its associated conceptual representation, which subsequently facilitates visual processing of its (congruent) word form. When they looked at the effects of the cue before the interaction with the target word, they found that congruent picture cues indeed successively enhanced activation in left middle temporal cortex, ventro-medial prefrontal cortex and visual cortex (Dikker and Pylkkanen, 2013). In addition, also category conditions were included, however no congruency effects in either early or later time-windows were observed for these conditions. Thus, Dikker and Pylkkanen also found that only conceptual information at the exemplar level, but not at the category level, affected early sensory processing. Note however that an alternative explanation for the early sensory effects in our study might be the fact that for exemplar cue conditions, incongruent targets were more probable than congruent targets.

Puri and Wojciulik used fMRI to investigate whether category expectations affect neural processing in visual areas (Puri et al., 2009). In a cue-target matching task with category cues ("face" or "house", 70% valid) and pictures of faces and houses, they observed a larger difference between preferred and non-preferred targets after congruent compared to incongruent cues (e.g., higher activation in FFA for face target after face cue relative to a place cue). In our study, no such effect of category cues on early and/or higher-order visual areas was found. This discrepancy might be explained by the fact that Puri and Wojciulik used predictive cues, which has been shown to elicit effects in (early) sensory cortices (Esterman and Yantis, 2009; Kok et al., 2012a; Summerfield et al., 2008). In our design however, the category cues were irrelevant and non-predictive for the semantic categorization task on the target picture, since we believe this reveals the most genuine effect of language. When word cues predict what visual information will most likely be presented, it is not exclusively the linguistic influence on perception that is at stake, since the effects are not specific to the semantic content but might also be found for arbitrary symbolic cues. As a consequence, our non-predictive cues might have resulted in a weaker linguistic signal and no activation of a perceptual template.

Complementing the fMRI results, our behavioral data showed that both congruent exemplar and category cues speed up perceptual categorization relative to incongruent conditions. Puri and Wojciulik also investigated whether category and exemplar expectations affect behavior (Puri and Wojciulik, 2008). In one experiment, they presented participants with congruent or incongruent exemplar name cues (75% valid) followed by pictures of famous faces or places and found that RTs were faster after congruent cues than after incongruent cues. In our experiment, although the likelihood of seeing a congruent target picture after the cue was instead 16% (since all six target pictures occurred equally often after each of the exemplar cues) we obtained the same results. In addition, we found that RTs were faster for incongruent exemplar within-category cues (EC-IW) than for incongruent between-category cues (EC-IB), suggesting that an exemplar cue does not only prime its associated visual representation, but also activates a category expectation, replicating the findings of Puri and Wojciulik (Puri and Wojciulik, 2008).

However, it should be noted that the difference between EC-IW and EC-IB conditions could alternatively be attributed to a response priming effect.

In another experiment with only (predictive) category cues (Puri and Wojciulik, 2008), Puri and Wojciulik did not observe congruency effects, while we did observe an RT advantage for congruent relative to incongruent category cues even though our category cues had no predictive relationship with the subsequent target. Possibly, this discrepancy could be explained by the fact that we used a semantic categorization task at the category level ("Does the target depict an animal or a tool?") whereas Puri and Wojciulik used a perceptual discrimination task (normal vs. distorted target pictures)(see also Puri et al., 2009).

For completeness we tested whether congruency effects differed between animal and tool targets. Behavioral congruency effects were similar for animal and for tool target pictures. In the fMRI experiment we found no selective congruency effects for animal or tool targets in the ventral or dorsal stream, respectively. Only the bilateral PFC showed larger activation for congruent relative to incongruent targets for animal relative to tool targets. Since our experiment was not designed to look at differences between animal and tool pictures, we had no a priori hypotheses and we would like to leave open the interpretation of these findings for future experiments.

In addition to our cue-target conditions, we included cue-only conditions in our design to assess whether and where category and exemplar cues activate a perceptual template independent of interactions with visual stimuli. However, no visual or 'language' areas were differentially activated for exemplar compared to category cues. Only the lPFC showed a stronger activation for category than exemplar cues. This finding possibly reflects response activation in the category, but not in the exemplar cue conditions, since the task required participants to make a semantic categorization decision at the category level. Other studies did find cue-related effects in visual areas (Dikker and Pylkkanen, 2013; Peelen and Kastner, 2011; Puri et al., 2009). For example, Peelen and Kastner studied the neural mechanisms underlying visual search in natural scenes (Peelen and Kastner, 2011). A symbolic cue indicated whether participants had to detect people or cars and was in 66% of the cases followed by a target scene whereas in the remaining, cue-only trials, no scene was presented. A multivariate correlation analysis revealed that category-specific activity patterns were present in EVC, LOC, and in mPFC.

We varied the typicality of the target pictures to test whether category cues activate a perceptual template of a typical category member compared with an atypical category member, which would be predicted by the 'prototype theory' (Mervis and Rosch, 1981; Rosch, 1973), This hypothesis has been empirically tested in behavioral studies, in which typical compared to atypical items resulted in quicker and more accurate responses (Mervis and Rosch, 1981). In addition, EEG studies show that atypical words elicit a larger N400 than typical items (Heinze et al., 1998; Stuss et al., 1988) and that additional posterior components (P160, N300) are affected by typical compared to atypical pictures (Barrett and Rugg, 1990; Hauk et al., 2007). However, our experimental manipulation did not result in a replication of these classic typicality effects. As a consequence, no differences in congruency effects between the different typicality conditions were found in the behavioral or fMRI experiment, in contrast to previous studies (Liu et al., 2013; Lupyan, 2008; Lupyan and Spivey, 2010b). Although the pre-test provided us with items

with clearly different typicality ratings, a couple of factors might have made the typicality manipulation ineffective. First, we used a limited stimulus set and we presented these stimuli multiple times. Second, we intended to match the stimuli on lexical frequency, as a result of which the typical stimuli in our set (elephant and hammer) did in fact not represent the actual most typical animal and tool.

To conclude, we provide further evidence for the feed-forward model of language-perception interactions. Congruent relative to incongruent semantic cues affect categorization performance of target pictures by showing a trend of increasing activity in the lMTG, an area involved in semantic processing. On top of that, our data suggest that the mechanisms underlying language-perception interactions might differ for semantic cues at different levels of the conceptual hierarchy. Exemplar cues may enable the activation of a detailed perceptual template, preparing sensory cortices for the processing of ensuing visual information, as reflected by our finding that incongruent exemplar cues elicit higher activation in the lEVC compared to congruent conditions. Category cues, on the other hand, might not provide specific information about what is coming up next and therefore interact with the visual information only at a later, conceptual processing stage. Thus, our findings provide a suggestion of a possible solution to the debate on the locus of the effect of language on perception by demonstrating that there may not be one single neural mechanism underlying language-perception interactions. Instead, the locus of these effects might depend on the specificity of linguistic information.

6

EMBODIED COGNITION: TAKING THE NEXT STEP

Roel M. WILLEMS and Jolien C. FRANCKEN

Recent years have seen a large amount of empirical studies related to 'embodied cognition'. While interesting and valuable, there is something dissatisfying with the current state of affairs in this research domain. Hypotheses tend to be underspecified, testing in general terms for embodied versus disembodied processing. The lack of specificity of current hypotheses can easily lead to an erosion of the embodiment concept, and result in a situation in which essentially any effect is taken as positive evidence. Such erosion is not helpful to the field and does not do justice to the importance of embodiment. Here we want to take stock, and formulate directions for how it can be studied in a more fruitful fashion. As an example we will describe few example studies that have investigated the role of sensori-motor systems in the coding of meaning ('embodied semantics'). Instead of focusing on the dichotomy between embodied and disembodied theories, we suggest that the field move forward and ask how and when sensori-motor systems and behavior are involved in cognition.

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6.1. INTRODUCTION: EXCITING EMBODIMENT

IN the last two decades, cognitive science has embraced the thesis of 'embodiment'. Embodied cognition stresses the intertwined nature of thinking and acting, and as such is an antidote to the traditional divide between cognition on the one hand and perception and action on the other. The excitement about embodiment within cognitive science lies mainly in its promise to destroy the traditional 'sandwich' (or 'hamburger') model of cognitive processing, with its strict perception-cognition-action scheme (e.g., Hurley, 2001). The sandwich model regards 'thinking' as the real stuff (the beef so to say), and takes perception and action as separated slave systems, providing input to cognitive processors (perception) and executing its commands (action). Instead, embodied cognition stresses that perception and action are directly relevant for our thinking, and that it is a mistake to regard them as separate. The thesis comes in various formats, and a more in depth coverage is beyond the scope of this article (e.g., Barsalou, 1999; Clark, 1997; Gallagher, 2005; Noe, 2004; O'Regan, 1992; van Gelder, 1995; Wheeler, 2005; Wilson, 2002).

In this paper we want to take stock and see what embodiment has done for a particular research domain in cognitive science, namely the study of semantic representations. With respect to semantic representations, embodied cognition is related to the claim of modality-specific versus abstract representations, in which modality-specific views predict sensori-motor cortex to be constitutive of conceptual representations (see Kiefer and Pulvermuller, 2012, for an excellent recent overview). This being an opinion paper, it is by no means our intention to give an overview of the field. Instead we highlight certain studies, where we could have chosen others. Of particular importance is that we have chosen to ignore the neuropsychological literature regarding semantic representations (see e.g., Caramazza and Mahon, 2003; Gainotti, 2000; Kiefer and Pulvermuller, 2012).

6.2. THE EROSION OF A CONCEPT: THE CASE OF EMBODIED SEMANTICS REPRESENTATIONS

OFTEN embodied cognition is defined very broadly. When we for example look at experiments investigating 'embodied semantics', an important prediction is that understanding sensori-motor concepts leads to activation of sensori-motor cortices. So when people read about hand and foot actions, parts of the motor cortex involved in moving the hands and the feet are activated (e.g., Hauk et al., 2004; Tettamanti et al., 2005). Although interesting from the sandwich model perspective, it is unfortunate that the main hypothesis often does not go beyond predicting 'involvement' of sensori-motor cortices (see also Binder and Desai, 2011; Chatterjee, 2010).

An illustration of this lack of specificity is how easily embodied cognition can capture strikingly different findings. For instance, Buccino et al. (2005) used single-pulse TMS to stimulate the hand or foot/leg motor area while participants were listening to sentences expressing foot and hand actions. Reaction times (RTs) and motor evoked potentials (MEPs) were specifically modulated for the effector involved in the described action: A hand-action related sentence produced decreased MEPs in the hand area and slower RTs when subjects responded with their hand. The authors conclude that the processing of language modulates the activity of the motor system in an effector specific way. However, in another TMS study with a similar design Pulvermuller et al. (2005) report that faster

RTs are observed to hand/arm words after stimulation of the hand area. It is striking that although the results are opposite (slower vs. faster RTs), both are taken as confirmation of the embodied semantics theory. Instead, the researchers could have elaborated more about the reason of their divergent findings. For instance, maybe the differences arise because the interference occurs at a decision making level after semantic analysis (Chatterjee, 2010; Mahon and Caramazza, 2008). By formulating more specific hypotheses, e.g., here on the direction of the effect and the underlying mechanism, these findings could have been more informative. It strikes us as disappointing to not go beyond the conclusion of involvement of cortical motor areas; the pattern of results suggests that something more interesting is going on than motor cortex activation in response to action words. One is left with the question: What result would be taken as evidence against embodied cognition?

Another sign of an underspecified theory is that similar findings can be interpreted as evidence in favor as well as against embodiment. Take the studies of Saygin et al. (2010) and Bedny et al. (2008). First, Saygin and colleagues showed activation of perceptual (visual) areas when subjects were reading sentences describing motion. More specifically, they found increased BOLD levels in motion sensitive area hMT+/V5 when participants read sentences like "The wild horse crossed the barren field" versus "The black horse stood in the barren field" (Saygin et al., 2010). Second, in the study of Bedny et al. (2008) participants judged pairs of words that implied motion (animals, e.g., "the horse", "the dog"), had intermediate implied motion (tools, e.g., "the sword", "the axe"), or had little implied motion (natural kinds, e.g., "the bush", "the pebble"). These authors did not find modulation of hMT+/V5 activity for words with different motion ratings. Regions within posterior lateral temporal cortex were more active when comparing verbs and nouns, independent of the amount of motion associations of the words.

A general theory of embodiment would have predicted both studies to find modulation in area hMT+/V5 related to amount of motion expressed in the materials. The fact that the one study does observe such modulation, and the other does not is an interesting clue to the context-dependence of sensory cortex activations during language comprehension (or as Saygin and colleagues put it: "The choice of task and stimuli can influence the power to detect modulations of hMT+/V5 by linguistic events" (Saygin et al., 2010, p. 2486). Instead, what happens is that one set of authors interpret their findings as in line with embodied cognition, and the other set of authors interprets their findings as evidence against embodiment, since they show that retrieval of sensory motor features is not obligatory during word comprehension (Bedny et al., 2008). The differences in their findings can probably be attributed to the differences in design. However, both studies generalize their results to the question of whether it supports an embodied or disembodied account, and it is in this interpretation stage that opposite conclusions are drawn.

Many experiments are driven by the 'embodied versus disembodied' distinction. This is not a fruitful approach, and in the next section we will show that such a broad distinction does not do justice to the experimental findings that are available. To foreshadow our conclusion: Instead of quarreling about embodied versus disembodied, the field should take the next step and ask the question when and how sensori-motor cortices play a role in understanding.

6.3. TAKING STOCK: EMBODIED SEMANTICS

WHEN we take a bird's eye perspective towards experiments studying sensori-motor cortex involvement when participants read or listen to language describing sensori-motor events (action and visual language), a few things stand out:

- Sensori-motor cortices can be activated during language comprehension. For instance, cortical motor hand areas can be activated when participants read verbs related to hand actions (e.g., Hauk et al., 2004; Tettamanti et al., 2005)
- These sensori-motor activations can be fast (e.g., Pulvermuller and Shtyrov, 2005)
- Changing the activation level (via training or with TMS) of the motor system can influence processing of action-related language, suggesting a functional role (e.g., Glenberg et al., 2008; Willems et al., 2011)
- Some studies do not replicate sensori-motor activations when participants listen to action-language (e.g., Postle et al., 2008)
- Sensori-motor involvement is dependent on task and linguistic context (e.g., Papeo et al., 2009; Sato et al., 2008)

Of these findings, the latter one deserves more attention than it has gotten so far: Sensori-motor cortex involvement during understanding of action and perceptual language is task- and context-dependent. For instance, it has been shown that the motor system is differently modulated depending on the experimental task. In a study by Sato et al. (2008) hand-action verbs interfered with button presses when participants performed a semantic task, but this was not the case when they performed a lexical decision task. Similarly, in an elegant study Papeo and colleagues reported modulation of hand MEPs during reading of hand-action verbs when single pulse TMS was applied, but again only during an explicit semantic categorization task (on action-relatedness) but not during a syllable detection task (Papeo et al., 2009).

Another example of context-dependence is provided by Raposo et al. (2009) who showed that activation in motor cortex varied depending on the way verbs were presented: When verbs were viewed in isolation ("kick") or in literal sentences ("kick the ball") motor cortex was activated, but when the verbs were presented in idiomatic contexts ("kick the bucket"), no motor or premotor activation was present (see also Aziz-Zadeh et al. (2006) but see Boulenger et al. (2009). van Dam et al. (2012a) varied the linguistic context in a different way: They instructed participants to focus either on the action or on the color aspect of a word's referent. Activation in action- and motion-related areas was higher in the former than in the latter condition. The authors suggest that the 'action' context emphasized action properties of the object and that therefore the corresponding action features were relevant in constituting the concept.

6.4. CONCLUSION

SO on the one hand, the state of affairs is favorable to embodied semantics: There can be involvement of sensori-motor cortices in understanding action and perceptual

language. This is an important insight and definitely constitutes a way forward in our thinking about the neural basis of conceptual knowledge (see Kiefer and Pulvermuller, 2012, for overview). But the involvement of sensori-motor cortex in conceptual representations is of a more complex nature than a simple binary 'yes' or 'no'. Investigating 'an involvement' of sensori-motor cortices in conceptual knowledge was perhaps a good first step, but needs to be followed up by more specific hypotheses. Future research needs to be more specific on when and how sensori-motor cortices are involved in language understanding. One reason for this is that current findings are too easily interpreted as confirming embodied accounts (see also Chatterjee, 2010). A second motivation is the fact that several studies show the context-dependence of sensorimotor involvement in language understanding. Computational models can be important in making the operations that take place in sensori-motor cortices more explicit, and the field should take more advantage of those (e.g., Chersi et al., 2010). Only with such specificity can embodied cognition make progress and will the concept retain its value.

7

GENERAL DISCUSSION

Jolien C. FRANCKEN

Even comparatively simple acts of perception are very much more at the mercy of the social patterns called words than we might suppose (Sapir, 1921, p. 210)

7.1. DISCUSSION OF RESULTS

THE current work has investigated whether, where and how language affects visual perception. The empirical results from Chapter 2 - 5 provide converging evidence for the hypothesis that language affects perception by the automatic feed-forward integration of perceptual and semantic material in language areas of the brain.

7.1.1. SUMMARY

In Chapter 2 - 4, we used congruent and incongruent linguistic cues (e.g., "rise", "fall") in combination with a visual motion paradigm to study the behavioral and neural effects of language-perception interactions. We found that participants were faster and more accurate when the direction implied by the motion word was congruent with the direction of the visual motion stimulus. Interestingly, in Chapter 2, the speed benefit was present only for motion stimuli that were presented in the right visual field (RVF). With fMRI we were able to identify the neural locus of the congruency effects. Both in Chapter 2 and in Chapter 4 we observed a neural counterpart of the behavioral facilitation effects in the left middle temporal gyrus (lMTG). The motion-selective visual cortex did not show any congruency effect, even when the motion words were attended (Chapter 4).

In the third chapter, we proposed two competing models of language-perception interactions: A feedback and a feed-forward model. To test the models, we included unaware linguistic information by backward masking of the motion words, which disrupts feedback processing. Masked words did still affect visual motion perception, in line with the feed-forward model and the fMRI results from Chapter 2 and Chapter 4. In Chapter 5, we found that cues at different levels of the conceptual hierarchy, i.e., the category ("animal") and exemplar ("elephant") levels, both affected response times to target pictures in a semantic categorization task. Again, the lMTG was found as the neural counterpart of this congruency effect. In addition, incongruent exemplar cues elicited higher activation in the left early visual cortex relative to incongruent conditions, providing some evidence for the hypothesis that only exemplar cues activate a perceptual template.

These studies inform the question on the locus of language-perception interactions in an important way. In contrast to earlier studies, we used experimental designs including both linguistic and visual material, to be able to look at the online effect of language on visual perception. This contrasts with approaches in which only linguistic stimuli (e.g., motion words, action verbs), or on the other hand, only visual stimuli (e.g., colored squares) were used. In addition, only a few studies have used neuroimaging methods to directly investigate the neural mechanisms underlying the interactions between linguistic and perceptual information (Hirschfeld et al., 2011; Landau et al., 2010; Sadaghiani et al., 2009).

7.1.2. LEVEL AND MECHANISM

What is the picture that emerges from the four chapters together? First, in line with an increasing number of studies (Landau et al., 2010; Lupyan et al., 2010; Meteyard et al., 2007; Winawer et al., 2007), we find reliable effects of language on perception. Even when words are non-predictive, irrelevant, unattended and even unaware, language affects visual detection, discrimination or categorization. This demonstrates that language-perception

interactions are automatic, rather than strategic processes. Thierry and colleagues provided evidence for this notion as well (Thierry et al., 2009). They studied implicit influences of language-specific color terminology on perception of different shades of blue and green in Greek (who have two different terms to refer to light blue and dark blue) and English native speakers. Participants performed an oddball shape detection task on blocks of light blue and dark blue, or light green and dark green stimuli. Within one block the most frequent stimulus was a light or dark circle and the remaining stimuli were circles with a contrasting luminance (deviant), e.g., dark if the standard was light. The visual mismatch negativity, an electrophysiological index of automatic and pre-attentive change detection, was similar for blue and green deviant stimuli during an oddball shape detection task in English participants, but was significantly larger for blue than green deviant stimuli in native speakers of Greek. This result might be explained by the fact that Greek participants perceived the luminance deviants as more different in the blue than in the green blocks. In contrast to earlier categorization and discrimination studies (Gilbert et al., 2006; Tan et al., 2008), here color was task-irrelevant and moreover, the authors report that none of the participants highlighted the critical stimulus dimension tested (luminance) or reported verbalizing the colors.

Second, all of our studies show a striking convergence in showing that the lMTG plays a crucial role in the integration of linguistic and visual information. Both in the context of low-level visual motion perception and of higher-level object categorization, our fMRI investigations showed higher activity in lMTG for congruent relative to incongruent conditions. The lMTG is part of the left-lateralized language network and is known to be involved in both lexical retrieval including word semantics and multisensory processing and integration (Beauchamp et al., 2004; Hagoort et al., 2009; Menenti et al., 2011; Noppeney et al., 2008; Schneider et al., 2008). The finding that lMTG is activated more strongly for congruent relative to incongruent conditions might reflect a semantic matching process between the linguistic information and the visual information, when the latter is translated into a lexical concept. This idea is in line with previous findings showing that the lMTG is involved in conceptual integration, whereas another important area in the language network of the brain, the lIFG, is activated during language processes involving 'unification' (Hagoort et al., 2009).

Others studying the effects of language on perception reported the involvement of temporal areas as well. Ting Siok et al. (2009) reported that perception of between-category colors relative to within-category colors activated the lMTG. Tan et al. (2008) found that perceptual identification of easy-to-name colors activated the left pSTG more strongly than hard-to-name colors. Sadaghiani and colleagues also found that the left pSTG was sensitive to the congruency of direction words (e.g., "left") and visual motion stimuli, showing more activation for incongruent compared to congruent conditions (Sadaghiani et al., 2009).

Interestingly, also outside of the field of language-perception interactions it has been argued that multisensory integration might happen at a conceptual rather than at a sensory level. Faivre et al. (2014) demonstrated that unconscious auditory and unconscious visual information is integrated by showing that it affects RTs to a subsequent target stimulus, providing evidence for unconscious multisensory integration. Noel et al. (2015) however argue that rather than an interaction at the sensory level, e.g., in superior tempo-

ral or parietal regions, this finding can better be explained by an unconscious semantic comparison of congruence of semantic information. The two independent sensory representations would refer to the same object and therefore activate a common semantic concept. Interestingly, they hypothesize that the neural locus of semantic integration would be the inferior frontal cortex, while we rather find involvement of lMTG.

Third, we found that visual areas show a consistent lack of sensitivity for the congruence between linguistic and visual information. This is in contrast to earlier studies and theoretical proposals (Dikker and Pylkkanen, 2011, 2013; Hirschfeld et al., 2011; Landau et al., 2010; Lupyan, 2012a; Saygin et al., 2010; Thierry et al., 2009). First, corresponding with top-down theories of visual perception, words could induce an expectation about the visual world, thereby automatically recruiting the relevant sensory areas. In line with this, Hirschfeld et al. (2011) found that ERPs to incongruent conditions differed from congruent conditions in a sentence-picture verification task around 170 ms and 400 ms after picture onset. The early effect suggests an effect of language on perception during visual processing. Dikker and Pylkkanen used MEG and provided similar evidence for an early interaction by showing that incongruent picture primes affect perception of visually presented words around 100ms over occipital sensors (Dikker and Pylkkanen, 2011). In addition, around 250-400 ms a difference over left-hemisphere sensors was observed. However, some of these results interpreted within the 'sensory level' framework could also be explained by the 'conceptual level' account, since differences between conditions after 100 ms could also reflect the rapid feed-forward integration of visual information and linguistic information (Thierry et al., 2009). Effects in visual areas might have arisen after an interaction at a later (conceptual) stage (see also Eger et al., 2007; Gilbert et al., 2008).

An alternative mechanism that would predict language-perception interactions in sensory areas is embodied simulation, according to which words themselves might recruit the visual cortex. This hypothesis claims that for instance words describing motion are partly represented in the corresponding perceptual areas that process the actual visual stimuli the words describe (Barsalou et al., 2003; Glenberg and Kaschak, 2003; Revill et al., 2008; Saygin et al., 2010). Some studies suggested that this is the case (Rueschemeyer et al., 2010; Saygin et al., 2010) however others failed to find involvement of early sensory areas and rather showed that posterior temporal areas are activated during comprehension of motion language (Bedny et al., 2008; Dravida et al., 2013; Wallentin et al., 2011). Moreover, critics argued that activation in sensory areas might be a downstream consequence of effects in language areas instead of an essential part of linguistic representations (Mahon and Caramazza, 2008). Interestingly, while embodied cognition aims to find evidence for involvement of sensori-motor cortices in semantic representation, we provide evidence for the opposite idea: language-processing areas are involved in visual perception.

A third cognitive mechanism for language-perception interactions, which would also predict involvement of early sensory areas, is visual mental imagery. According to the theory of embodied semantics, mental imagery might even be a component of language understanding in general (Saygin et al., 2010) and this process might explain the findings in sensory areas after reading motion language (but see Willems et al., 2010). However, our findings in Chapter 3 demonstrated that masked words can still influence perception, and therefore mental imagery cannot be the standard mechanism underlying effects of

language on perception.

Interestingly, only in Chapter 5 we observed a hint into the direction that words that describe upcoming visual information in a more detailed way might induce a perceptual template, while language at a more categorical level might not. Thus, an alternative explanation for the lack of effects in sensory areas might be that a verbal prime does not necessarily lead to a useful perceptual template, since there is a nearly infinite variety of specific visual images that could correspond to e.g., the word "rise" (Esterman and Yantis, 2009). This explanation does probably not apply to the study in Chapter 5, since the stimulus set was limited which might have made the activation of a perceptual template after an exemplar cue more likely.

Thus, the empirical evidence from the four chapters together suggests that language-perception interactions occur at a post-sensory stage. While the fMRI results point to the lMTG as the neural locus of these effects, i.e., a conceptual stage of processing, it is possible that later decision, response or memory stages are affected as well, similar to the mechanisms underlying the Stroop effect (MacLeod, 1991). For instance, motion words could have primed perceptual decisions about motion direction at a higher-order decision level. However, the fact that we obtained language-perception effects lateralized to the RVF in Chapter 2 is incompatible with this account since only the language areas are lateralized to the left hemisphere. In addition, in all three fMRI experiments the congruency effects were limited to the lMTG (except for Chapter 5, where we found an additional effect in the lEVC). No decision or conflict-related brain areas where activated for the incongruent conditions relative to the congruent conditions or the reverse contrast, which makes the decision-level hypothesis less likely.

7.1.3. LATERALIZATION OF EFFECTS

We hypothesized that the effects of language on perception might be stronger for stimuli presented in the right visual field (RVF), i.e., processed in the left hemisphere. This lateralization is explained by the fact that information from the right visual field would have preferential access to the left-lateralized language system (Gilbert et al., 2006; Klemfuss et al., 2012; Regier and Kay, 2009). Previous studies found evidence for this hypothesis with both behavioral and neuroimaging paradigms (Drivonikou et al., 2007; Fonteneau and Davidoff, 2007; Gilbert et al., 2006, 2008; Holmes et al., 2009; Kwok et al., 2011; Liu et al., 2009, 2010; Mo et al., 2011; Ting Siok et al., 2009).

In the first three empirical chapters, we therefore presented the visual stimuli in either the LVF or RVF to be able to study whether this would affect the effects of language on perception. Only in Chapter 2 we found a reliable difference between congruency effects in the LVF and RVF, by showing that RTs were speeded for RVF stimuli but not for LVF stimuli. However in the studies in Chapter 3 and Chapter 4, in which we made the linguistic signal stronger by adding a categorization task to the motion words in a small percentage of the trials, the effect was present in both hemispheres. In addition, studies investigating the development of color language acquisition show that the picture is more complex. For instance, Franklin and colleagues compared infant and adult performance on a color visual search task (Franklin et al., 2008). Whereas adults showed categorical color perception lateralized to the RVF in line with earlier findings (Gilbert et al., 2006), pre-linguistic infants showed no categorical color perception in the RVF, but only in the

LVF.

Therefore, rather than an all-or-nothing phenomenon, we propose that lateralization of language-perception interactions may depend on the extent to which attention is directed to the language stimuli. Unattended stimuli may 'remain local' and thereby only affect visual processing in the same hemisphere leading to unilateral effects, whereas attended stimuli might be 'broadcasted' to other neural processors resulting in larger and bilateral effects (Dehaene and Changeux, 2011). Future studies are required to directly assess the potential effects of attention on language-perception interactions.

7.2. OPEN QUESTIONS

I believe the most important contribution of the studies in this thesis is that they ask for a more nuanced picture of the effects of language on perception. Since evidence for the cognitive and neural mechanisms underlying these effects is mixed, I suggest that rather than asking what is the mechanism or locus of language-perception interactions, we might ask whether the mechanism depends on different characteristics of these interactions.

A similar argument was made by Willems and Francken in the context of embodied semantics in Chapter 6. Here, we showed that this theories' main hypothesis often does not go beyond predicting 'involvement' of sensori-motor cortices and that many experiments are driven by the 'embodied versus disembodied' distinction. As a result of this lack of specificity, the theory can capture opposite findings, and similar findings are interpreted as evidence in favor as well as against embodiment. We argued that the field should instead ask the question when and how sensori-motor cortices play a role in understanding, since the experimental findings demonstrate that sensori-motor cortex involvement during understanding of action and perceptual language is task- and context-dependent (Rueschemeyer et al., 2010; van Dam et al., 2012b).

In the field of language-perception interactions, a similar argument can be put forward. Just like research into embodied semantics shows that sensori-motor cortices are sometimes involved in understanding action and perceptual language, a couple of studies have shown that effects of language on perceptions are accompanied by modulations in neural activity in sensory areas. However, it is now time to take the next step and ask how and under what conditions sensory cortices are involved in language-perception interactions.

7.2.1. CONCEPT HIERARCHY

One of such factors, which we studied in Chapter 5, might be the effect of concept hierarchy. We hypothesized that words from a higher level in the concept hierarchy, e.g., "animal", might interact with visual information at a later stage than words from a lower level, e.g., "elephant". The rationale behind this is that category cues would not activate a specific perceptual template in the sensory areas, because it is uncertain which animal will appear. In the case of an exemplar cue, the interaction might instead occur at the sensory level. Although our results are inconclusive, they showed a congruency effect in lMTG when exemplar and category cues were combined, and in addition an effect in lEVC for exemplar cues, in line with our hypothesis and previous studies (Dikker and Pylkkanen, 2011; Puri and Wojciulik, 2008). Puri and Wojciulik also used exemplar and

category cues and found effects on discrimination performance only for exemplar cues (Puri and Wojciulik, 2008). In a follow-up experiment however, they also obtained effects on RTs for category cues (Puri et al., 2009). Hence, further research is needed to elucidate the commonalities and differences of effects of linguistic information at different levels of the conceptual hierarchy on perception.

7.2.2. TYPICALITY

A question that we were unable to answer in Chapter 5 is whether the typicality of the visual information affects language-perception interactions. If linguistic cues would activate a perceptual template of the most typical instance of their category, this might result in stronger or different interactions with more typical items relative to less typical items. For instance, typical visual stimuli might be affected by language at an early sensory stage, while atypical items might be affected only at a later semantic level. Typicality effects have been investigated in the context of language-perception interactions, however mostly in behavioral studies (Lupyan, 2008; Lupyan et al., 2007; Lupyan and Spivey, 2010b).

Lupyan and colleagues observed that spoken category cues, e.g., the word “five”, speeded up RTs for the numeral in a typical font relative to an atypical font (Lupyan et al., 2007; Lupyan and Spivey, 2010b). In addition, Lupyan found that typicality rating scores for pictures of chairs and lamps differed when the question included either the category name or the exemplar name ("How typical was that object" vs. "How typical was that chair")(Lupyan, 2008). Typical pictures were rated as more typical after the exemplar cue than after the category cue, while this effect was absent for atypical pictures.

Also non-linguistic visual cues affect perception of visual stimuli depending on typicality. Lupyan used a discrimination task with cat and dog silhouettes (Lupyan et al., 2010). Obviously, RTs were slower for within-category comparisons (e.g., two cats) than for between-category comparisons (e.g., a cat and a dog). Interestingly however, the size of this category effect was affected by the typicality of the first stimulus that was presented. When the first picture was a typical cat and the second an atypical cat, RTs were slower compared to when the atypical stimulus preceded the typical stimulus. According to the authors, the typical stimulus strongly activates the conceptual category to which it belongs, e.g. the category ’cats’, and this makes the second stimulus more ’cat-like’ which results in a smaller perceived difference between the first and the second stimulus, increasing discrimination RTs. On the other hand, when the first stimulus is an atypical cat, the conceptual category ’cats’ is less activated and does not change perception of the second stimulus.

Extending these behavioral studies, Liu et al. (2013) used fMRI in combination with a category verification task with word cues (category level, 50% valid) and picture targets . They found that atypical items elicited slower RTs and larger activity in the left and right superior frontal gyrus, inferior frontal gyrus, middle frontal gyrus, and right inferior parietal lobule, but no effects in visual areas. It would be interesting to test the typicality hypothesis in the context of language-perception interaction more directly in future studies.

7.2.3. PROBABILISTIC CUES

Another determinant for the mechanism underlying language-perception interactions might be the probabilistic relationship between the linguistic and visual information. In all of our studies, we have chosen to use non-predictive linguistic cues, since we believe this reveals the most genuine effect of language. When language is predictive, we believe that it is not exclusively the linguistic influence on perception that is at stake, since the effects are not specific to the semantic content anymore, but might also be found by using arbitrary symbolic cues. Yet, many studies investigating language-perception interactions did take this strategy, using one of two types of experimental paradigms.

The first kind of paradigm is very similar to the ones used in this thesis: A linguistic or symbolic cue is presented followed by a visual stimulus (e.g., a picture of an object). However, crucially, in these studies the cue is predictive for the upcoming stimulus. For instance, Esterman and Yantis used 100% valid visual cues in an object discrimination task with gradually appearing faces and houses in an fMRI study (Esterman and Yantis, 2009). Discrimination (gender for faces and structure for houses) was faster after valid compared to neutral cues. The fMRI results showed that in anticipation of the target stimulus, activity increased in higher-order category-specific visual areas in the temporal lobe but not in earlier extrastriate areas. One explanation that the authors provide for the absence of effects in early visual areas is the nature of the task, which required participants to prepare to see a member of an object category rather than a specific object.

Puri and Wojciulik also used fMRI to investigate whether category expectations affect neural processing face- and place-selective visual areas (Puri et al., 2009). In a cue-target matching task with 70% valid category cues ("face" or "house") and pictures of faces and houses, they observed a larger difference between preferred and non-preferred targets after congruent compared to incongruent cues was observed (e.g., higher activation in FFA for face target after face cue relative to a place cue). In contrast to these two studies reporting effects in (higher-order) visual areas, Eger et al. (2007) found that non-predictive word cues speed the recognition of objects that were slowly coming into focus, but this was not accompanied by anticipatory changes in early nor higher-order visual cortex, when controlling for speed of recognition.

The second type of paradigm including predictive cues targets the subjective experience or detection of visual stimuli rather than discrimination or categorization. Lupyan and Ward reported effects of language on the visibility of visual stimuli that are rendered invisible by means of inter-ocular flash-suppression (Lupyan and Ward, 2013). Presentation of a 75% valid verbal cue before an invisible image of an object changed object detection performance relative to an uninformative cue. When we compare this to a binocular rivalry study without a predictive association between cue and stimulus, actually here no effects (on initial dominance) were found (Pelekanos et al., 2011).

Thus, the probabilistic relationship between the linguistic and perceptual information might be an important factor accounting for many of the divergent findings with respect to the mechanism and level of language-perception interactions.

7.2.4. EXPERIMENTAL TASK

Similar to what can be observed in the field of embodied semantics, the experimental task might be an important factor influencing how language affects perception. For

instance, in many of the studies that we discussed participants performed a perceptual categorization task (Gilbert et al., 2006; Tan et al., 2008) and possibly benefited from a verbalizing strategy, which might have influence on the way in which linguistic and visual information interact (see also Thierry et al., 2009). Interestingly, in this thesis we used a variety of perceptual task ranging from detection, to discrimination, to categorization but we consistently observed that the lMTG was sensitive to the difference between congruent and incongruent conditions. This might suggest that language-perception interactions occur at the conceptual level regardless of the type of task.

7.2.5. TEMPORAL OVERLAP BETWEEN STIMULI

The temporal overlap between linguistic and perceptual information might affect the way language affects perception. In our first three empirical chapters, the motion words preceded the visual motion stimuli by 400 ms (stimulus onset asynchrony (SOA)) to make sure that the words were fully semantically analyzed (Hagoort et al., 2009). Meteyard et al. (2007) used an unsynchronized auditory presentation of words and visual stimuli, with blocks of motion words per motion direction and found congruency effects in *d'* and *C* but not in RTs. In another study, Meteyard et al. (2008) reversed the presentation of the visual stimuli and the motion words: Motion stimuli were followed by written words. At a threshold coherence level, RTs were slower when the direction of visual motion and of the word was incongruent. With supra-threshold motion, ERs were lower for control verbs than for congruent or incongruent verbs.

Pavan et al. (2013) varied the SOA parametrically from 0, to 150, 450, and 1000 ms. They found that congruency effects on *d'* and RTs were largest when the onsets of the motion words and the visual stimuli were 450 ms apart, thus when the words are semantically analyzed, in line with our findings. The prerequisite of a relatively long SOA suggests that the integration of visual and linguistic information occurs at the semantic level, and not at the sensory level (Pavan et al., 2013). In addition, their results show that the absence of an effect on *d'* in Chapter 2 is probably not the consequence of the relatively long SOA.

7.2.6. THE EFFECT OF ATTENTION

Attention is a factor that seems to play an ambiguous role. In Chapter 3 and Chapter 4, we found that paying attention to the motion words increased the behavioral effects relative to the findings in Chapter 2, however this manipulation did not result in more widespread neural effects. Brouwer and Heeger directly compared color perception in a color naming and a diverted attention task (Brouwer and Heeger, 2013). For the color-naming task in visual areas V4v and VO1 greater similarity between activity patterns evoked by stimulus colors within a perceptual category was observed, compared to between-category colors. This was not the case for the diverted attention task, although it should be noted that this may not be the most appropriate control condition.

7.2.7. THE ROLE OF SEMANTIC CONTEXT

Finally, the effects of language on perception might be context-dependent. van Dam et al. (2010) showed that motor activation after reading action-related words is not an automatic process, but is flexibly recruited dependent on the semantic context in which a word is presented. They used a go/no-go lexical decision task with target words that were

either presented in a semantic context that emphasized dominant functional use of an object or non-dominant action features. A facilitation effect in RTs was found when the functional use was congruent with the prepared response movement, however only when the semantic context emphasized corresponding motor properties. In another study, van Dam et al. showed that context (focus on action or on color aspect of object) also affected the modality-specific activation elicited by auditory presented words and the connectivity between auditory brain regions and regions coding action information (van Dam et al., 2012a,b). Effects of language on perception might be dependent on semantic context in a similar way.

7.2.8. CONCLUSION

From this discussion we can see that even though many people currently investigate the effects of language on perception in various ways, there are still numerous open questions. It appears that there are several ways in which language can affect perception, yet we do not yet know which factors are the most important ones. In this thesis, we used the same design multiple times, each time with only small modifications. I believe such an approach is necessary if we want to come to a full scientific understanding of the cognitive and neural mechanisms underlying language-perception interactions.

7.3. THE BIGGER PICTURE

ACCORDING to most cognitive neuroscientists, cognitive neuroscience can answer questions about the where (what neural structures implement the phenomenon?) and the how of cognitive phenomena (what representations and algorithms underlie the phenomenon?), in other words, the physical and the algorithmic level of explanation (Mack et al., 2013; Marr, 1982). Answering these questions is what I aimed to do with respect to the phenomenon that language affects perception. Our findings suggest that language modulates perception at the level of language areas, rather than at a sensory level of visual processing. From this result I reasoned that the conceptual categorization mechanism of perception is the most likely algorithm underlying these interactions. Here, I would like to elucidate this mechanism and compare it with an alternative proposal.

Subsequently, I would like to go beyond the realm of cognitive neuroscience and discuss the computational level, which includes not only the question of what the phenomenon is or does, but also why it does these things. In other words, it has been shown that language affects perception, but what could be the benefit of these interactions? And finally, I will extend my findings from the scientific level of explanation to society, by showing how this phenomenon affects human interactions, art, politics and even scientific inquiry itself.

7.3.1. ALGORITHMIC LEVEL: PERCEPTION IS CATEGORIZATION

I have discussed the possible mechanisms underlying language-perception interactions in section 1.4 and I argued that the conceptual categorization mechanism of perception best fits our experimental findings. According to this model, everything we perceive is automatically processed up to a semantic level. For instance, when you look around in your living room, the way you see the objects surrounding you is influenced by the

conceptual categories in which we carve them: Table, chair, plant, magazines, and windows. Potentially, then this conceptual representation might interact with a conceptual representation activated by concurrent linguistic input, which might increase the degree of semantic activation (Lupyan, 2012a). Luypan also proposed that language augments cognition, including perception:

> Verbal labels do not simply point or refer to non-linguistic concepts, but actively modulate object representations that are brought online during 'non-verbal' tasks (Lupyan, 2012b, p. 255)

Lupyan and others suggest that the mechanism underlying language-perception interactions is feedback to early sensory areas, and that perceptual experiences are actually 'perceptuo-linguistic experiences'. For instance, after learning a color name, seeing that color now rapidly activates its name. According to Lupyan, this information subsequently feeds back and modulates on-going conceptual and perceptual processing. Lupyan thinks the feedback effects of language on perception result from online top-down modulations rather than from permanent changes in bottom-up processing (Gilbert et al., 2006). This is in line with empirical findings from Brouwer and Heeger, who showed that the neural clustering of color representations is task-dependent (Brouwer and Heeger, 2013).

Although Lupyan's hypothesis can account convincingly for many of the empirical findings, I would like to argue that categorization of perception can also be explained by interactions at the conceptual level, and that feedback is not required, although it might be a later consequence of semantic activation. This model is in line with our results, indicating that only lMTG, and not the visual cortex, is sensitive to the congruency between visual and linguistic information. Moreover, it can account for the effects of unaware motion words on perception from Chapter 3 and Chapter 4. Finally, it is a simpler explanation than the feedback model, which requires both feed-forward activation of the conceptual level, and additionally subsequent feedback to visual areas.

7.3.2. COMPUTATIONAL LEVEL: WHY DOES LANGUAGE AFFECT PERCEPTION?

A WORLD WITH WORDS

What would be the functional consequence of the automatic conceptual categorization of everything we perceive? Can we see more or better if we have words to describe things? Evidence for this idea comes from cross-cultural studies in linguistics that I discussed earlier (Thierry et al., 2009; Winawer et al., 2007). For instance, the Russian language makes an obligatory distinction between light blue and dark blue, and as a result Russian speakers are quicker to distinguish light blue from dark blue shades compared to English speakers (Winawer et al., 2007). According to the conceptual categorization mechanism of perception, when you see two colored objects you automatically activate their color names, which makes it easier to discriminate them when the names are different, but more difficult when they have the same name. As a result of the fact that Russians have a more elaborate color terminology, one might argue that Russian speakers are able to see more fine-grained differences between colors.

This mechanism does also provide an explanation for the well-known urban legend about Eskimo's and their snow vocabulary. The first source of this story is Boas' Handbook of North American Indians (Boas, 1911). He states that while the English language has

only one, Eskimo's have actually four (and not more than hundred!) words for snow: aput ("snow on the ground"), gana ("falling snow"), piqsirpoq ("blowing snow") and qimuqsuq ("snowdrift"). From this observation, it does not follow necessarily that they also see the world differently (see also subsection 1.2.2). Maybe Eskimo's have more words for snow just because snow is an important part of their natural environment. According to Steven Pinker:

> It's probably for the same reason that bicycle mechanics have more words for parts of bicycles, and painters have more words for shades of mauve, and so on. When you're in the habit of dealing with different aspects of the world, and dealing with other people who are also dealing with those aspects, you're going to invent the words to be able to communicate them. And I think the fact that we invent slang, we invent jargon, we invent new figures of speech when we need to, shows that we have the idea first, and we think to ourselves, "How am I going to clothe this in words so I can make it clear to some other person?" (Pinker, 1998)

The fact that we learn words during development also enables or even forces us to guide our vision and attention to the world in a certain way. Remember for instance the study of Levinson (subsection 1.2.2) who found that some Aboriginal languages rely on absolute spatial reference frames (Levinson, 1996). People speaking these languages always need to maintain their orientation to be able to communicate properly. Boroditsky emphasizes how profoundly this difference affects social interactions:

> The normal greeting in Kuuk Thaayorre is "Where are you going?" and the answer should be something like "Southsoutheast, in the middle distance." If you don't know which way you're facing, you can't even get past "Hello." (Boroditsky, 2009)

Boroditsky showed that the excellent spatial capabilities of these Aboriginal groups also affects other representations that they use, for instance the representation of time (Boroditsky and Gaby, 2010). One way to test whether language actually changes what we perceive is to teach people new words and see whether this affects perception. Casasanto and colleagues showed that when English speakers learned new ways of talking about time, for instance to use size metaphors (as in Greek) their cognitive performance started to resemble that of Greek speakers (Casasanto et al., 2004). Lupyan investigated how the acquisition of nonsense names (e.g., "grecious") to refer to unfamiliar objects affected learning of these objects (Lupyan et al., 2007). He compared this to a situation in which people had to learn to discriminate the objects without being given words to name them. Indeed, people learned to classify objects more quickly when they also learned the names for the objects. Moreover, the effect was larger than when the objects were paired with non-verbal associations (location information). Apparently, language makes category distinctions more apparent or concrete.

Together, different studies suggest that we can see more or better if we have words to describe things. But what would happen at the opposite end of the spectrum? If you do not have the words to categorize or name the things around you, can't you see them at all?

A WORLD WITHOUT WORDS

If you do not have a name for an object, you cannot categorize it. As a consequence, you might not see the object properly. William James attempted to describe the experience of seeing something with and without a name:

> I went out for instance the other day and found that the snow just fallen had a very odd look, different from the common appearance of snow. I presently called it a 'micaceaous' look; and it seemed to me as if, the moment I did so, the difference grew more distinct and fixed than it was before. The other connotations of the word 'micaceous' dragged the snow farther away from ordinary snow and seemed even to aggravate the peculiar look in question. (James, 1890, p.484)

A unique opportunity to see how the world looks like without language was the experience of psychologist Schaller who encountered Ildefonso, a Mexican Indian. He was born deaf and had never been taught even the most basic language. Schaller attempted to teach him a comprehension of words, which turned out to be very difficult, but in the end she succeeded. She describes the moment that Ildefonso realized that words carry meaning:

> Ildefonso's face opened in excitement as he slowly pondered this revelation. His head turned to his left and very gradually back to his right. Slowly at first, then hungrily, he took in everything as though he had never seen anything before: the door, the bulletin board, the chairs, tables, students, the clock, the green blackboard, and me. (Schaller, 1991, p. 44-45)

One could ask: what about Ildefonso's perceptual experience before he met Schaller? And how do pre-linguistic infants or animals perceive the world? They are also able to see, recognize and categorize the world around them. This is true, however, words or category names potentially greatly facilitate categorization and abstraction (Lupyan et al., 2007).

7.3.3. THE POWER OF WORDS

The idea that language plays an important role in how we see the world relates also to many aspects of our society, such as politics, scientific discovery, and even art.

The grammatical gender of a word in an artist's native language predicts whether abstract entities such as death or victory are depicted as a man or a woman (Boroditsky, 2009). For example, German painters are more likely to paint death as a man, whereas Russian painters are more likely to paint death as a woman.

Lakoff has demonstrated that linguistic constructions such as metaphors affect how we see the world (Lakoff, 1987; Lakoff and Johnson, 1980). This psychological phenomenon is known as 'framing'. Framing is a powerful political tool that can be used to effectively change people's worldview. For instance, a metaphor such as "war on terror" activates negative feelings of fear and anxiety and as a consequence might increase the likelihood of conservative voting (Lakoff, 2008). A fictive extension of this idea was described in *1984*, the famous book by George Orwell (Orwell, 1949). The totalitarian Party invented a new language called Newspeak meant to diminish the range of thought. For

instance, the word "free" still existed in Newspeak but could not be used any more in terms of being able to do as one pleases, as in "free will" but only in terms of something not being possessed, e.g., "the field is free from weeds".

Fleck claimed that scientific discovery is only possible if we already possess the concepts that enable us to think and see that what we are looking for (Fleck, 1979). These concepts emerge from the 'thought style', the common ideas and knowledge existing in a scientific community. A scientist starting to investigate a new phenomenon is in the same situation as a layperson. A layperson does not know how a phenomenon looks like, how to recognize it, or how to discriminate between important aspects and unimportant details. An expert sees the matter differently, because she is familiarized with many examples through training and with a set of views on what the phenomenon is, how it evolves, etcetera. Therefore, Fleck states that scientists cannot start from collecting data:

> "To see" means: To recreate, at a suitable moment, a picture created by the mental collective to which one belongs (Fleck, 1986, p.78)

Thus, paralleling the ideas from the totalitarian Party in *1984*, language empowers us to see the world in a new, or even a completely different way.

The effects of language on perception are manifest outside of the cognitive neuroscience lab as well. Therefore, the scientific study of this phenomenon might enable us not only to understand how we perceive the world, but also how we see ourselves, others and society. Ultimately, investigations into the effects of language on perception might benefit from their own insights, by emphasizing the important role of language in scientific discovery (see also Francken and Slors, 2014).

REFERENCES

Anderson, E., Siegel, E. H., Bliss-Moreau, E., and Barrett, L. F. (2011). The visual impact of gossip. *Science*, 332(6036):1446–8.

Ansorge, U., Kunde, W., and Kiefer, M. (2014). Unconscious vision and executive control: how unconscious processing and conscious action control interact. *Consciousness and Cognition*, 27:268–87.

Athanasopoulos, P., Dering, B., Wiggett, A., Kuipers, J. R., and Thierry, G. (2010). Perceptual shift in bilingualism: Brain potentials reveal plasticity in pre-attentive colour perception. *Cognition*, 116(3):437–43.

Aziz-Zadeh, L. and Damasio, A. (2008). Embodied semantics for actions: findings from functional brain imaging. *Journal of Physiology-Paris*, 102(1-3):35–9.

Aziz-Zadeh, L., Fiebach, C. J., Naranayan, S., Feldman, J., Dodge, E., and Ivry, R. B. (2008). Modulation of the ffa and ppa by language related to faces and places. *Social Neuroscience*, 3(3-4):229–38.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., and Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, 16(18):1818–23.

Barrett, S. E. and Rugg, M. D. (1990). Event-related potentials and the semantic matching of pictures. *Brain and Cognition*, 14(2):201–12.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4):577–609.

Barsalou, L. W. (2008). Grounded cognition. *Annual Reviews in Psychology*, 59:617–45.

Barsalou, L. W., Kyle, S. W., Barbey, A. K., and Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences*, 7(2):84–91.

Beauchamp, M. S., Lee, K. E., Argall, B. D., and Martin, A. (2004). Integration of auditory and visual information about objects in superior temporal sulcus. *Neuron*, 41(5):809–23.

Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., and Saxe, R. (2008). Concepts are more than percepts: the case of action verbs. *Journal of Neuroscience*, 28(44):11347–53.

Berlin, B. and Kay, P. (1969). *Basic colour terms: Their universality and evolution*. University of California Press, Berkeley.

Binder, J. R. and Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11):527–36.

Boas, F. (1911). *Handbook of American Indian languages*. Government Print Office (Smithsonian Institution, Bureau of American Ethnology), Washington.

BonJour, L. (2001). Epistemological problems of perception.

Boroditsky, L. (2009). *How Does Our Language Shape the Way We Think?*, pages 116–129. Vintage Books, New York, Toronto.

Boroditsky, L. and Gaby, A. (2010). Remembrances of times east: absolute spatial representations of time in an australian aboriginal community. *Psychological Science*, 21(11):1635–9.

Boroditsky, L., Schmidt, L., and Phillips, W. (2003). *Sex, syntax, and semantics*, page 61–80. MIT Press, Cambridge, Massachussetts.

Boulenger, V., Hauk, O., and Pulvermuller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex*, 19(8):1905–14.

Boutonnet, B., Athanasopoulos, P., and Thierry, G. (2012). Unconscious effects of grammatical gender during object categorisation. *Brain Research*, 1479:72–9.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4):433–6.

Brouwer, G. J. and Heeger, D. J. (2013). Categorical clustering of the neural representation of color. *Journal of Neuroscience*, 33(39):15454–65.

Brown, A. M., Lindsey, D. T., and Guckes, K. M. (2011). Color names, color categories, and color-cued visual search: sometimes, color perception is not categorical. *Journal of Vision*, 11(12).

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., and Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined tms and behavioral study. *Brain Research*, 24(3):355–63.

Caramazza, A. and Mahon, B. Z. (2003). The organization of conceptual knowledge: the evidence from category-specific semantic deficits. *Trends in Cognitive Sciences*, 7(8):354–61.

Carpenter, R. (1988). *Movement of the eyes*. Pion Limited, London, 2nd edition.

Casasanto, D., Boroditsky, L., Phillips, W., Greene, J., Goswami, S., Bocanegra-Thiel, S., and Santiago-Diaz, I. (2004). How deep are effects of language on thought? time estimation in speakers of english, indonesian, greek, and spanish. In Kenneth, F., Gentner, D., and Reiger, T., editors, *26th Annual Cognitive Science Society*. Lawrence Erlbaum.

Chatterjee, A. (2010). Disembodying cognition. *Language and Cognition*, 2(1):79–116.

Chersi, F., Thill, S., Ziemke, T., and Borghi, A. M. (2010). Sentence processing: linking language to motor chains. *Frontiers in Neurorobotics*, 4.

Clark, A. (1997). *Being there: putting brain, body and world together again*. MIT Press, Cambridge, MA.

Dehaene, S. and Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2):200–27.

Dehaene, S. and Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*, 79(1-2):1–37.

Dehaene, S., Sergent, C., and Changeux, J. P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *PNAS*, 100(14):8520–5.

Del Cul, A., Baillet, S., and Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *Plos Biology*, 5(10):e260.

Desender, K., Van Lierde, E., and Van den Bussche, E. (2013). Comparing conscious and unconscious conflict adaptation. *Plos One*, 8(2).

Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews in Neuroscience*, 18:193–222.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, 91(1):176–80.

Dikker, S. and Pylkkanen, L. (2011). Before the n400: Effects of lexical-semantic violations in visual cortex. *Brain and Language*, 118(1-2):23–8.

Dikker, S. and Pylkkanen, L. (2013). Predicting language: Meg evidence for lexical preactivation. *Brain and Language*, 127(1):55–64.

Dils, A. T. and Boroditsky, L. (2010). Visual motion aftereffect from understanding motion language. *PNAS*, 107(37):16396–400.

Dravida, S., Saxe, R., and Bedny, M. (2013). People can understand descriptions of motion without activating visual motion brain regions. *Frontiers in Psychology*, 4.

Drivonikou, G. V., Kay, P., Regier, T., Ivry, R. B., Gilbert, A. L., Franklin, A., and Davies, I. R. (2007). Further evidence that whorfian effects are stronger in the right visual field than the left. *PNAS*, 104(3):1097–102.

Eger, E., Henson, R. N., Driver, J., and Dolan, R. J. (2007). Mechanisms of top-down facilitation in perception of visual objects studied by fmri. *Cerebral Cortex*, 17(9):2123–33.

Esterman, M. and Yantis, S. (2009). Perceptual expectation evokes category-selective cortical activity. *Cerebral Cortex*, 20(5):1245–53.

Fahrenfort, J. J., Scholte, H. S., and Lamme, V. A. F. (2007). Masking disrupts reentrant processing in human visual cortex. *Journal of Cognitive Neuroscience*, 19(9):1488–1497.

Faivre, N., Mudrik, L., Schwartz, N., and Koch, C. (2014). Multisensory integration in complete unawareness: Evidence from audiovisual congruency priming. *Psychological Science*, 25(11):2006–16.

Fleck, L. (1935/1986). *Scientific Observation and Perception in General*, page 59–78. Boston Studies in the Philosophy of Science. D. Reidel Publishing Company, Dordrecht, Boston, Lancester, Tokyo, 87 edition.

Fleck, L. (1979). *Genesis and Development of a Scientific Fact*. University of Chicago Press, Chicago, London.

Fodor, J. A. (1975). *The Language Of Thought*. Crowell Press.

Fonteneau, E. and Davidoff, J. (2007). Neural correlates of colour categories. *Neuroreport*, 18(13):1323–7.

Forstmann, B. U., Jahfari, S., Scholte, H. S., Wolfensteller, U., van den Wildenberg, W. P. M., and Ridderinkhof, K. R. (2008). Function and structure of the right inferior frontal cortex predict individual differences in response inhibition: A model-based approach. *Journal of Neuroscience*, 28(39):9790–6.

Francken, J. C., Gaal, S., and de Lange, F. P. (2011). Immediate and long-term priming effects are independent of prime awareness. *Consciousness and Cognition*, 20(4):1793–800.

Francken, J. C., Kok, P., Hagoort, P., and de Lange, F. P. (2015a). The behavioral and neural effects of language on motion perception. *Journal of Cognitive Neuroscience*, 27(1):175–84.

Francken, J. C., Meijs, E. L., Hagoort, P., Van Gaal, S., and De Lange, F. P. (2015b). Exploring the automaticity of language-perception interactions: Effects of attention and awareness. *Scientific Reports*.

Francken, J. C., Meijs, E. L., Ridderinkhof, O. M., Hagoort, P., De Lange, F. P., and Van Gaal, S. (2015c). Manipulating word awareness dissociates feed-forward from feedback models of language-perception interactions. *Neuroscience of Consciousness*, 1.

Francken, J. C. and Slors, M. (2014). From commonsense to science, and back: the use of cognitive concepts in neuroscience. *Consciousness and Cognition*, 29:248–58.

Franklin, A., Drivonikou, G. V., Clifford, A., Kay, P., Regier, T., and Davies, I. R. (2008). Lateralization of categorical perception of color changes with color term acquisition. *PNAS*, 105(47):18221–5.

Friston, K. J. (2005). A theory of cortical responses. *Philosophical transactions of the Royal Society of London*, 360(1456):815–36.

Friston, K. J., Holmes, A., Poline, J. B., Price, C. J., and Frith, C. D. (1996). Detecting activations in pet and fmri: Levels of inference and power. *NeuroImage*, 4(3):223–35.

Friston, K. J., Rotshtein, P., Geng, J. J., Sterzer, P., and Henson, R. N. (2006). A critique of functional localisers. *NeuroImage*, 30(4):1077–87.

Gainotti, G. (2000). What the locus of brain lesion tells us about the nature of the cognitive defect underlying category-specific disorders: a review. *Cortex*, 36(4):539–59.

Gallagher, S. (2005). *How the body shapes the mind*. Oxford University Press, Oxford.

Gallese, V. and Lakoff, G. (2005). The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22(3):455–79.

Gilbert, A. L., Regier, T., Kay, P., and Ivry, R. B. (2006). Whorf hypothesis is supported in the right visual field but not the left. *PNAS*, 103(2):489–94.

Gilbert, A. L., Regier, T., Kay, P., and Ivry, R. B. (2008). Support for lateralization of the whorf effect beyond the realm of color discrimination. *Brain and Language*, 105(2):91–8.

Gilbert, C. D. and Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, 14(5):350–63.

Glenberg, A. and Kaschak, M. (2003). *The body's contribution to language*. The Psychology of Learning and Motivation. Academic Press, San Diego, California.

Glenberg, A. M., Sato, M., and Cattaneo, L. (2008). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology*, 18(7):R290–1.

Greenwald, A. G., Klinger, M. R., and Schuh, E. S. (1995). Activation by marginally perceptible ("subliminal") stimuli: dissociation of unconscious from conscious cognition. *Journal of Experimental Psychology General*, 124(1):22–42.

Gregory, R. L. (1980). Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 290(1038):181–197.

Hagoort, P., Baggio, G., and Willems, R. M. (2009). *Semantic unification*, pages 819–836. MIT Press, Cambridge, MA, 4th edition.

Hannula, D. E., Simons, D. J., and Cohen, N. J. (2005). Imaging implicit perception: promise and pitfalls. *Nature Reviews Neuroscience*, 6(3):247–55.

Hauk, O., Johnsrude, I., and Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2):301–7.

Hauk, O., Patterson, K., Woollams, A., Cooper-Pye, E., Pulvermuller, F., and Rogers, T. T. (2007). How the camel lost its hump: the impact of object typicality on event-related potential signals in object decision. *Journal of Cognitive Neuroscience*, 19(8):1338–53.

Hauk, O., Shtyrov, Y., and Pulvermuller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology-Paris*, 102(1-3):50–8.

Heinze, H. J., Muente, T. F., and Kutas, M. (1998). Context effects in a category verification task as assessed by event-related brain potential (erp) measures. *Biological Psychology*, 47(2):121–35.

Hirschfeld, G., Zwitserlood, P., and Dobel, C. (2011). Effects of language comprehension on visual processing - meg dissociates early perceptual and late n400 effects. *Brain and Language*, 116(2):91–6.

Holmes, A., Franklin, A., Clifford, A., and Davies, I. (2009). Neurophysiological evidence for categorical perception of color. *Brain and Cognition*, 69(2):426–34.

Holmes, K. J. and Wolff, P. (2012). Does categorical perception in the left hemisphere depend on language? *Journal of Experimental Psychology General*.

Hurley, S. (2001). Perception and action: Alternative views. *Synthese*, 129:3–40.

Indefrey, P. and Levelt, W. (2000). *The neural correlates of language production*, pages 845–65. MIT Press, Cambridge, MA.

Indefrey, P. and Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition*, 92(1-2):101–44.

Jackendoff, R. (2002). *Foundations of Language: Brain, Meaning, Grammar, Evolution*. Oxford University Press, New York.

Jacoby, L. L. (1991). A process dissociation framework - separating automatic from intentional uses of memory. *Journal of Memory and Language*, 30(5):513–541.

James, W. (1890). *The principles of psychology*. Dover Publications, New York.

Jeffreys, H. (1961). *Theory of Probability*. Oxford University Press, Oxford, third edition.

Jiang, J., van Gaal, S., Bailey, K., Chen, A. T., and Zhang, Q. L. (2013). Electrophysiological correlates of block-wise strategic adaptations to consciously and unconsciously triggered conflict. *Neuropsychologia*, 51(13):2791–8.

Kaschak, M. P., Madden, C. J., Therriault, D. J., Yaxley, R. H., Aveyard, M., Blanchard, A. A., and Zwaan, R. A. (2005). Perception of motion affects language processing. *Cognition*, 94(3):B79–89.

Kay, P. and Kempton, W. (1984). What is the sapir-whorf hypothesis. *American Anthropologist*, 86(1):65–79.

Kiefer, M. and Pulvermuller, F. (2012). Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*, 48(7):805–25.

Klemfuss, N., Prinzmetal, W., and Ivry, R. B. (2012). How does language change perception: a cautionary note. *Frontiers in Psychology*, 3:78.

Kok, P., Jehee, J. F. M., and de Lange, F. P. (2012a). Less is more: Expectation sharpens representations in the primary visual cortex. *Neuron*, 75(2):265–70.

Kok, P., Rahnev, D., Jehee, J. F. M., Lau, H. C., and de Lange, F. P. (2012b). Attention reverses the effect of prediction in silencing sensory signals. *Cerebral Cortex*, 22(9):2197–206.

Kosslyn, S. M., Ganis, G., and Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2(9):635–42.

Kouider, S. and Dehaene, S. (2007). Levels of processing during non-conscious perception: a critical review of visual masking. *Philosophical Transactions of the Royal Society B Biological Sciences*, 362(1481):857–75.

Kunde, W. (2003). Sequential modulations of stimulus-response correspondence effects depend on awareness of response conflict. *Psychonomic Bulletin & Review*, 10(1):198–205.

Kunde, W., Reuss, H., and Kiesel, A. (2012). Consciousness and cognitive control. *Advances in Cognitive Psychology*, 8(1):9–18.

Kwok, V., Niu, Z., Kay, P., Zhou, K., Mo, L., Jin, Z., So, K. F., and Tan, L. H. (2011). Learning new color names produces rapid increase in gray matter in the intact adult human cortex. *PNAS*, 108(16):6686–8.

Lakoff, G. (1987). *Women, fire, and dangerous things*. University Of Chicago Press, Chicago, London.

Lakoff, G. (2008). *The Political Mind*. Viking Penguin, London.

Lakoff, G. and Johnson, M. (1980). *Metaphors We Live By*. University of Chicago Press, Chicago, London.

Lamme, V. A. and Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, 23(11):571–9.

Lamme, V. A., Zipser, K., and Spekreijse, H. (2002). Masking interrupts figure-ground signals in v1. *Journal of Cognitive Neuroscience*, 14(7):1044–53.

Landau, A. N., Aziz-Zadeh, L., and Ivry, R. B. (2010). The influence of language on perception: listening to sentences about faces affects the perception of faces. *Journal of Neuroscience*, 30(45):15254–61.

Lau, H. C. and Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *Journal of Neuroscience*, 27(21):5805–11.

Leung, H. C., Skudlarski, P., Gatenby, J. C., Peterson, B. S., and Gore, J. C. (2000). An event-related functional mri study of the stroop color word interference task. *Cerebral Cortex*, 10(6):552–60.

Levinson, S. C. (1996). Language and space. *Annual Reviews in Anthropology*, 25:353–82.

Liu, C., Tardif, T., Wu, H. Y., Monk, C. S., Luo, Y. J., and Mai, X. Q. (2013). The representation of category typicality in the frontal cortex and its cross-linguistic variations. *Brain and Language*, 127(3):415–27.

Liu, Q., Li, H., Campos, J. L., Wang, Q., Zhang, Y., Qiu, J., Zhang, Q., and Sun, H. J. (2009). The n2pc component in erp and the lateralization effect of language on color perception. *Neuroscience Letters*, 454(1):58–61.

Liu, Q., Li, H., Jennifer, L. C., Teeter, C., Tao, W. D., Zhang, Q. L., and Sun, H. J. (2010). Language suppression effects on the categorical perception of colour as evidenced through erps. *Biological Psychology*, 85(1):45–52.

Lund, T. E., Norgaard, M. D., Rostrup, E., Rowe, J. B., and Paulson, O. B. (2005). Motion or activity: their role in intra- and inter-subject variation in fmri. *NeuroImage*, 26(3):960–4.

Lupyan, G. (2008). From chair to "chair": a representational shift account of object labeling effects on memory. *Journal of Experimental Psychology General*, 137(2):348–69.

Lupyan, G. (2012a). Linguistically modulated perception and cognition: the label-feedback hypothesis. *Frontiers in Psychology*, 3:54.

Lupyan, G. (2012b). What do words do? toward a theory of language-augmented thought. *Psychology of Learning and Motivation*, 57:255–297.

Lupyan, G., Rakison, D. H., and McClelland, J. L. (2007). Language is not just for talking - redundant labels facilitate learning of novel categories. *Psychological Science*, 18(12):1077–83.

Lupyan, G. and Spivey, M. J. (2010a). Making the invisible visible: verbal but not visual cues enhance visual detection. *PLoS One*, 5(7):e11452.

Lupyan, G. and Spivey, M. J. (2010b). Redundant spoken labels facilitate perception of multiple items. *Attention Perception & Psychophysics*, 72(8):2236–53.

Lupyan, G., Thompson-Schill, S. L., and Swingley, D. (2010). Conceptual penetration of visual processing. *Psychological Science*, 21(5):682–91.

Lupyan, G. and Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *PNAS*, 110(35):14196–201.

Mack, M. L., Preston, A. R., and Love, B. C. (2013). Decoding the brain's algorithm for categorization from its neural implementation. *Current Biology*, 23(20):2023–7.

MacLeod, C. M. (1991). Half a century of research on the stroop effect: an integrative review. *Psychological Bulletin*, 109(2):163–203.

Macmillan, N. A. and Creelman, C. D. (2005). *Detection Theory: A User's Guide*. Mahwah, N.J.: Lawrence Erlbaum Associates, 2 edition.

Mahon, B. Z. and Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology-Paris*, 102(1-3):59–70.

Malotki, E. (1983). *Hopi Time: A Linguistic Analysis of the Temporal Concepts in the Hopi Language*, volume Studies and Monographs 20 of *Trends in Linguistics*. Mouton Publishers., Berlin, New York, Amsterdam.

Marr, D. (1982). *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. Freeman, San Francisco.

Masharov, M. and Fischer, M. H. (2006). Linguistic relativity: Does language help or hinder perception? *Current Biology*, 16(8):R289–91.

Menenti, L., Gierhan, S. M. E., Segaert, K., and Hagoort, P. (2011). Shared language: overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional mri. *Psychological Science*, 22(9):1173–82.

Merikle, P. M., Smilek, D., and Eastwood, J. D. (2001). Perception without awareness: perspectives from cognitive psychology. *Cognition*, 79(1-2):115–134.

Mervis, C. B. and Rosch, E. (1981). Categorization of natural objects. *Annual Review of Psychology*, 32:89–115.

Meteyard, L., Bahrami, B., and Vigliocco, G. (2007). Motion detection and motion verbs: language affects low-level visual perception. *Psychological Science*, 18(11):1007–13.

Meteyard, L., Cuadrado, S. R., Bahrami, B., and Vigliocco, G. (2012). Coming of age: a review of embodiment and the neuroscience of semantics. *Cortex*, 48(7):788–804.

Meteyard, L., Zokaei, N., Bahrami, B., and Vigliocco, G. (2008). Visual motion interferes with lexical decision on motion words. *Current Biology*, 18(17):R732–3.

Meyer, A. S., Belke, E., Telling, A. L., and Humphreys, G. W. (2007). Early activation of object names in visual search. *Psychonomic Bulletin & Review*, 14(4):710–6.

Mitterer, H., Horschig, J. M., Musseler, J., and Majid, A. (2009). The influence of memory on perception: it's not what things look like, it's what you call them. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35(6):1557–62.

Mo, L., Xu, G., Kay, P., and Tan, L. H. (2011). Electrophysiological evidence for the left-lateralized effect of language on preattentive categorical perception of color. *PNAS*, 108(34):14026–30.

Naccache, L., Blandin, E., and Dehaene, S. (2002). Unconscious masked priming depends on temporal attention. *Psychological Science*, 13(5):416–24.

Noe, A. (2004). *Action in perception*. MIT Press, Cambridge, MA.

Noel, J. P., Wallace, M., and Blake, R. (2015). Cognitive neuroscience: Integration of sight and sound outside of awareness? *Current Biology*, 25(4):R157–9.

Noppeney, U., Josephs, O., Hocking, J., Price, C. J., and Friston, K. J. (2008). The effect of prior visual information on recognition of speech and sounds. *Cerebral Cortex*, 18(3):598–609.

O'Regan, J. K. (1992). Solving the "real" mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology*, 46(3):461–88.

Orwell, G. (1949). *1984*. Secker and Warburg, London.

Papeo, L., Vallesi, A., Isaja, A., and Rumiati, R. I. (2009). Effects of tms on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One*, 4(2):e4508.

Pavan, A., Skujevskis, M., and Baggio, G. (2013). Motion words selectively modulate direction discrimination sensitivity for threshold motion. *Frontiers in Human Neuroscience*, 7:134.

Peelen, M. V. and Kastner, S. (2011). A neural basis for real-world visual search in human occipitotemporal cortex. *PNAS*, 108(29):12125–30.

Pelekanos, V. and Moutoussis, K. (2011). The effect of language on visual contrast sensitivity. *Perception*, 40(12):1402–12.

Pelekanos, V., Roumani, D., and Moutoussis, K. (2011). The effects of categorical and linguistic adaptation on binocular rivalry initial dominance. *Frontiers in Human Neuroscience*, 5:187.

Pinker, S. (1998). Language and consciousness part 1: Are our thoughts constrained by language? with steven pinker, ph.d.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., and De Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *NeuroImage*, 43(3):634–44.

Pulvermuller, F., Hauk, O., Nikulin, V. V., and Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, 21(3):793–7.

Pulvermuller, F. and Shtyrov, Y. an Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, 17(6):884–92.

Puri, A. M. and Wojciulik, E. (2008). Expectation both helps and hinders object perception. *Vision Research*, 48(4):589–97.

Puri, A. M., Wojciulik, E., and Ranganath, C. (2009). Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex. *Brain Research*, 1301:89–99.

Rahnev, D., Lau, H., and de Lange, F. P. (2011). Prior expectation modulates the interaction between sensory and prefrontal regions in the human brain. *Journal of Neuroscience*, 31(29):10741–8.

Raposo, A., Moss, H. E., Stamatakis, E. A., and Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia*, 47(2):388–96.

Regier, T. and Kay, P. (2009). Language, thought, and color: Whorf was half right. *Trends in Cognitive Sciences*, 13(10):439–46.

Revill, K. P., Aslin, R. N., Tanenhaus, M. K., and Bavelier, D. (2008). Neural correlates of partial lexical activation. *PNAS*, 105(35):13111–5.

Richardson, D. C., Spivey, M. J., Barsalou, L. W., and McRae, K. (2003). Spatial representations activated during real-time comprehension of verbs. *Cognitive Science*, 27(5):767–80.

Ridderinkhof, K. R. (2002). *Activation and suppression in conflict tasks: Empirical clarification through distributional analyses*, volume XIX of *Common Mechanisms in Perception and Action*, pages 494–519. Oxford University Press, Oxford.

Rosch, E. H. (1973). Natural categories. *Cognitive Psychology*, 4(3):328–350.

Rouder, J. N., Speckman, P. L., Sun, D. C., Morey, R. D., and Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, 16(2):225–37.

Rueschemeyer, S. A., Glenberg, A. M., Kaschak, M. P., Mueller, K., and Friederici, A. D. (2010). Top-down and bottom-up contributions to understanding sentences describing objects in motion. *Frontiers in Psychology*, 1:183.

Sadaghiani, S., Hesselmann, G., and Kleinschmidt, A. (2009). Distributed and antagonistic contributions of ongoing activity fluctuations to auditory stimulus detection. *Journal of Neuroscience*, 29(42):13410–7.

Sapir, E. (1921). *Language: An introduction to the study of speech*. Harcourt, Brace and company, New York.

Sato, M., Mengarelli, M., Riggio, L., Gallese, V., and Buccino, G. (2008). Task related modulation of the motor system during language processing. *Brain and Language*, 105(2):83–90.

Saygin, A. P., McCullough, S., Alac, M., and Emmorey, K. (2010). Modulation of bold response in motion-sensitive lateral temporal cortex by real and fictive motion sentences. *Journal of Cognitive Neuroscience*, 22(11):2480–90.

Schaller, S. (1991). *A man without words*. University of California Press, London.

Schneider, T. R., Debener, S., Oostenveld, R., and Engel, A. K. (2008). Enhanced eeg gamma-band activity reflects multisensory semantic matching in visual-to-auditory object priming. *NeuroImage*, 42(3):1244–54.

Segall, M., Campbell, D., and Herskovits, M. (1966). *The influence of culture on visual perception*. The Bobbs-Merrill Company, Indianapolis.

Snijders, T. M., Petersson, K. M., and Hagoort, P. (2010). Effective connectivity of cortical and subcortical regions during unification of sentence structure. *NeuroImage*, 52(4):1633–44.

Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J., Petersson, K. M., and Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: an fmri study using word-category ambiguity. *Cerebral Cortex*, 19(7):1493–503.

Snodgrass, J. G. and Vanderwart, M. (1980). Standardized set of 260 pictures - norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, 6(2):174–215.

Spruyt, A., De Houwer, J., Everaert, T., and Hermans, D. (2012). Unconscious semantic activation depends on feature-specific attention allocation. *Cognition*, 122(1):91–95.

Stanfield, R. A. and Zwaan, R. A. (2001). The effect of implied orientation derived from verbal context on picture recognition. *Psychological Science*, 12(2):153–6.

Stuss, D. T., Picton, T. W., and Cerri, A. M. (1988). Electrophysiological manifestations of typicality judgment. *Brain and Language*, 33(2):260–72.

Summerfield, C. and de Lange, F. P. (2014). Expectation in perceptual decision making: neural and computational mechanisms. *Nature Reviews Neuroscience*, 15(11):745–56.

Summerfield, C. and Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences*, 13(9):403–9.

Summerfield, C., Egner, T., Greene, M., Koechlin, E., Mangels, J., and Hirsch, J. (2006). Predictive codes for forthcoming perception in the frontal cortex. *Science*, 314(5803):1311–4.

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., and Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, 11:1004 – 1006.

Swoyer, C. (2003). Relativism.

Tan, L. H., Chan, A. H., Kay, P., Khong, P. L., Yip, L. K., and Luke, K. K. (2008). Language affects patterns of brain activation associated with perceptual decision. *PNAS*, 105(10):4004–9.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., and Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, 17(2):273–81.

Thierry, G., Athanasopoulos, P., Wiggett, A., Dering, B., and Kuipers, J. R. (2009). Unconscious effects of language-specific terminology on preattentive color perception. *PNAS*, 106(11):4567–70.

Ting Siok, W., Kay, P., Wang, W. S., Chan, A. H., Chen, L., Luke, K. K., and Hai Tan, L. (2009). Language regions of brain are operative in color perception. *PNAS*, 106(20):8140–5.

Trabant, J. (2000). *How relativistic are Humboldts "Weltansichten"?* John Benjamins Publishing Company.

Tsushima, Y., Sasaki, Y., and Watanabe, T. (2006). Greater disruption due to failure of inhibitory control on an ambiguous distractor. *Science*, 314(5806):1786–8.

van Dam, W. O., Rueschemeyer, S. A., Lindemann, O., and Bekkering, H. (2010). Context effects in embodied lexical-semantic processing. *Frontiers in Psychology*, 1:150.

van Dam, W. O., van Dijk, M., Bekkering, H., and Rueschemeyer, S. A. (2012a). Flexibility in embodied lexical-semantic representations. *Human Brain Mapping*, 33(10):2322–2333.

van Dam, W. O., van Dongen, E. V., Bekkering, H., and Rueschemeyer, S. A. (2012b). Context-dependent changes in functional connectivity of auditory cortices during the perception of object words. *Journal of Cognitive Neuroscience*, 24(10):2108–19.

van Gaal, S., de Lange, F. P., and Cohen, M. X. (2012). The role of consciousness in cognitive control and decision making. *Frontiers in Human Neuroscience*, 6.

van Gaal, S. and Lamme, V. A. (2012). Unconscious high-level information processing: implication for neurobiological theories of consciousness. *Neuroscientist*, 18(3):287–301.

van Gaal, S., Lamme, V. A., and Ridderinkhof, K. R. (2010). Unconsciously triggered conflict adaptation. *PLoS One*, 5(7):e11508.

van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., and Lamme, V. A. F. (2008). Frontal cortex mediates unconsciously triggered inhibitory control. *Journal of Neuroscience*, 28(32):8053–62.

van Gaal, S., Ridderinkhof, K. R., van den Wildenberg, W. P., and Lamme, V. A. (2009). Dissociating consciousness from inhibitory control: evidence for unconsciously triggered response inhibition in the stop-signal task. *Journal of Experimental Psychology: Human Perception and Performance*, 35(4):1129–39.

van Gelder, T. (1995). *The distinction between mind and cognition*. Academica Sinica, Taipei, Taiwan.

Von Helmholtz, H. (1910/1925). *Treatise on Physiological Optics*. Dover Press, New York.

Wallentin, M., Nielsen, A. H., Vuust, P., Dohn, A., Roepstorff, A., and Lund, T. E. (2011). Bold response to motion verbs in left posterior middle temporal gyrus during story comprehension. *Brain and Language*, 119(3):221–5.

Watson, A. B. and Pelli, D. G. (1983). Quest: a bayesian adaptive psychometric method. *Perception & Psychophysics*, 33(2):113–20.

Weiskopf, D. A. (2010). Embodied cognition and linguistic comprehension. *Studies in History and Philosophy of Science*, 41(3):294–304.

Wheeler, M. (2005). *Reconstructing the cognitive world*. MIT Press, Cambridge, MA.

Whorf, B. L. (1956). *An American Indian model of the universe*. MIT Press, Cambridge, Massachussetts.

Willems, R. M. and Casasanto, D. (2011). Flexibility in embodied language understanding. *Frontiers in Psychology*, 2.

Willems, R. M. and Francken, J. C. (2012). Embodied cognition: Taking the next step. *Frontiers in Psychology*, 3.

Willems, R. M., Labruna, L., D'Esposito, M., Ivry, R., and Casasanto, D. (2011). A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. *Psychological Science*, 22(7):849–854.

Willems, R. M., Toni, I., Hagoort, P., and Casasanto, D. (2010). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience*, 22(10):2387–400.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin and Review*, 9(4):625–636.

Winawer, J., Witthoft, N., Frank, M. C., Wu, L., Wade, A. R., and Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. *PNAS*, 104(19):7780–5.

Witzel, C. and Gegenfurtner, K. R. (2011). Is there a lateralized category effect for color? *Journal of Vision*, 11(12):16.

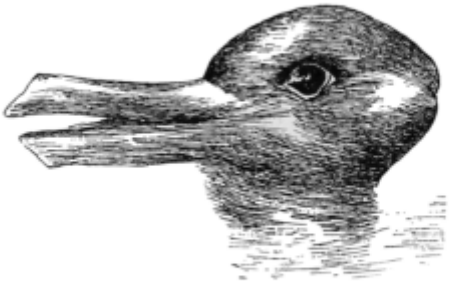
Worsley, K. J. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, 4:58–73.

Zhou, K., Mo, L., Kay, P., Kwok, V. P., Ip, T. N., and Tan, L. H. (2010). Newly trained lexical categories produce lateralized categorical perception of color. *PNAS*, 107(22):9974–8.

Zwaan, R. A., Stanfield, R. A., and Yaxley, R. H. (2002). Language comprehenders mentally represent the shapes of objects. *Psychological Science*, 13(2):168–71.

NEDERLANDSE SAMENVATTING

Hoe zien wij de wereld? In mijn beleving neem ik alles waar wat er om me heen te zien, te horen en te ervaren is, en zie ik de dingen zoals ze zijn. Maar is dat wel zo? Neem het plaatje hieronder (figuur 7.1). Hier kun je zowel een eend als een haas in zien. Maar terwijl je wisselt van 'eend' naar 'haas' en van 'haas' naar 'eend', verandert er niets in het plaatje.



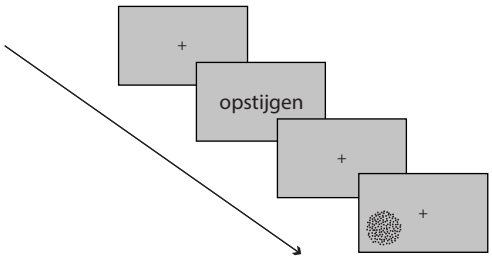
Figuur 7.1: Eend en haas. Wikimedia Commons.

Dit fenomeen, dat we zelf op de wereld projecteren wat we willen zien, geldt eigenlijk voor alles wat we waarnemen. Onze verwachtingen en ook onze aandacht voor dingen bepalen mede wat we zien, en voor een veel groter deel dan we zelf beseffen. Onze hersenen proberen continu te voorspellen wat er het volgende moment zal gebeuren op basis van wat we eerder hebben meegemaakt.

Wat heeft dit met taal te maken? In mijn onderzoek heb ik bestudeerd of taal ook zo'n factor is die mede bepaalt hoe we de wereld zien. Van jongs af aan beschrijven we de wereld door middel van taal, waardoor er sterke associaties zijn ontstaan tussen woorden en wat ze beschrijven. Ik heb onderzocht hoe sterk deze associaties zijn en hoe en waar dit fenomeen plaatsvindt in de hersenen: het hersensignaal van het woord komt ergens een 'plaatje' tegen van wat je ziet, maar waar precies? Als je aan een haas denkt, wat gebeurt er dan vervolgens zodat je switcht van 'eend' naar 'haas'?

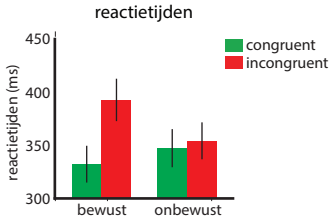
In de studie in hoofdstuk 2 hebben we onderzocht of het lezen van woorden die beweging uitdrukken, zoals "vallen" en "opstijgen", kan veranderen hoe je beweging waarneemt. Als je het woord "vallen" leest, zie je dan vervolgens bewegende stippen op een computerscherm vaker omlaag bewegen dan omhoog? Dit was inderdaad wat we vonden: wanneer het woord dezelfde bewegingsrichting beschreef ("vallen") als de richting van de bewegende stippen (omlaag), reageerden proefpersonen sneller én accurater dan

wanneer het woord de tegengestelde bewegingsrichting beschreef (“opstijgen”)(zie figuur 7.2). Dat is interessant, want de woorden hadden geen voorspellende waarde voor de richting van de stippen: na een “op”-woord volgde in de helft van de gevallen een beweging omhoog, en in de andere helft een beweging omlaag. Desondanks informeren deze irrelevante woorden onze perceptuele beslissingen.



Figuur 7.2: Proefpersonen zagen een grijs computerscherm met daarop eerst een woord (bijvoorbeeld - opstijgen") en kort daarna een cirkel met bewegende stippen, die omhoog of omlaag konden bewegen. Ze moesten vervolgens zo snel mogelijk kiezen wat de richting van de stippen was.

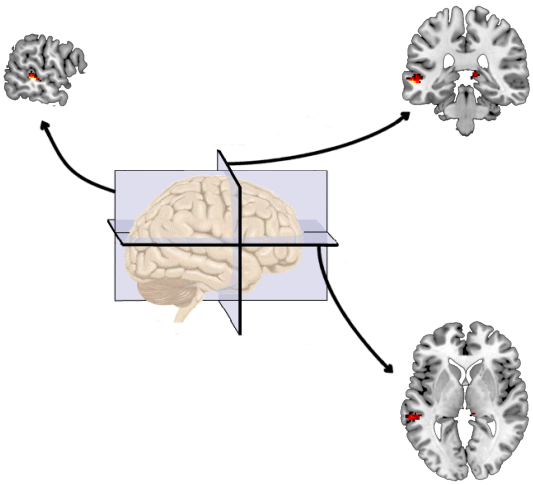
In hoofdstuk 3 testten we hoe automatisch de beïnvloeding van onze waarneming door taal verloopt. Een standaardmanier om dit te onderzoeken is het ‘maskeren’ van de woorden. Door een woord maar héél kort te laten zien (33 milliseconden) en net ervoor en erna een ‘masker’ te tonen (willekeurige letters, bijvoorbeeld “WJDBRT”) kun je het woord onbewust maken. Dat wil zeggen, de proefpersoon kan niet vertellen welk woord hij heeft gezien, maar het woord wordt wel gedeeltelijk verwerkt door het taalsysteem in de hersenen. Door de bewegingswoorden te maskeren en dus onbewust te maken, konden we onderzoeken of de woorden desondanks toch invloed zouden hebben op het waarnemen van de richting van bewegende stippen. En dat was inderdaad zo: zelfs als je de woorden niet bewust kan lezen, zorgen ze ervoor dat je sneller en beter beoordeelt of beweging omhoog of omlaag gericht is wanneer het woord dezelfde richting beschrijft (zie figuur 7.3).



Figuur 7.3: Reactietijden waren sneller wanneer het de richting die het woord beschreef en de bewegingsrichting van de stippen hetzelfde waren (congruent, in groen), dan wanneer deze verschillend waren (incongruent, in rood). Dit was ook het geval voor woorden die niet bewust waargenomen konden worden (rechts).

Naast deze effecten van taal op perceptuele beslissingen onderzochten we ook de onderliggende hersenprocessen die mogelijk maken dat je sneller en vaker correct re-

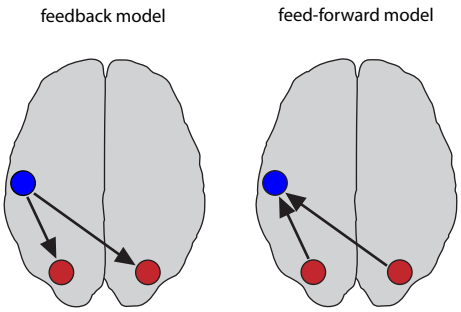
ageert op woorden die passen bij je wat je ziet. Om deze hersenprocessen in beeld te brengen, hebben we gebruik gemaakt van fMRI, een meetmethode die het zuurstofgebruik van hersencellen in beeld brengt. Zo kan je bekijken welke hersengebieden actief worden tijdens het uitvoeren van een bepaalde verrichting, zoals bewegen, rekenen of waarnemen. In hoofdstuk 2 lieten we proefpersonen daarom in de fMRI-scanner weer bewegingswoorden lezen in combinatie met het bekijken van bewegende stippen. De opdracht was dezelfde als in het eerder beschreven experiment: aangeven of de stippen omhoog of omlaag bewegen. Op deze manier konden we bekijken waar de hersenactiviteit verschilde tussen de condities waarin de woorden congruent waren met de beweging van de stippen (bijvoorbeeld öpstijgen"+ opwaartse beweging) en die condities waarin de woorden incongruent waren met de bewegingsrichting (bijvoorbeeld "neervallen"+ opwaartse beweging). We vonden dat er een verschil was in hersenactiviteit voor deze twee situaties in een gebied in de linker temporaalkwab (zie figuur 7.4). Dit hersengebied is betrokken bij het verwerken van de betekenis van taal, en ook bij het integreren van meerdere bronnen van conceptuele informatie.



Figuur 7.4: Een hersengebied in de linker temporaalkwab was meer actief wanneer de talige en visuele informatie congruent waren dan wanneer ze incongruent waren. De schaal loopt van geel (meer actief) naar rood (minder actief).

Ons fMRI-experiment toonde aan dat een verschil in verwerking in het taalsysteem in de hersenen ervoor zorgt dat perceptie van beweging sneller en beter gaat als talige en visuele informatie overeenstemmen. Waarom zou het taalsysteem betrokken zijn bij dit integratieproces? Is het niet logischer dat taal het visuele deel van de hersenen beïnvloedt? Sommige onderzoekers betogen van wel. Toch geeft niet alleen ons onderzoek in hoofdstuk 2, maar ook het feit dat we effecten van onbewuste woorden op perceptie vinden in hoofdstuk 3 ons reden om te denken dat er geen feedback-signalen van taal naar het visuele systeem gestuurd worden. Gemaskeerde informatie wordt namelijk alleen lokaal verwerkt, dus zij kan zich niet zomaar verspreiden naar een ander hersengebied - en daardoor word je je ook niet bewust van deze informatie. Het feit dat wij desalniettemin

een interactie tussen taal en perceptie zien voor onbewuste woorden, kan daarom alleen maar betekenen dat de visuele informatie verstuurd is naar het taalsysteem (zie figuur 7.5).

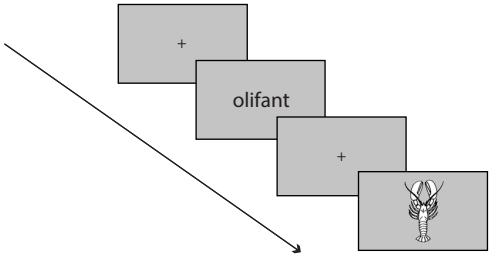


Figuur 7.5: Twee modellen van taal-perceptie interacties. Volgens het feedback model (links) wordt er talige informatie (in blauw) naar de visuele hersengebieden (in rood) gestuurd. Wij vinden echter bewijs voor het feed-forward model. Hier wordt visuele informatie verstuurd naar de taalgebieden in de linker hersenhelft.

In hoofdstuk 4 herhaalden we de experimentele opzet van hoofdstuk 3 in de fMRI-scanner, om te kijken of we onze bevindingen konden repliceren. Dat was inderdaad het geval: we vonden opnieuw dat een gebied in de linker temporaalkwab meer actief was wanneer de bewegingsrichting van de stippen en de richting beschreven door het woord congruent waren dan wanneer ze van elkaar verschilden. Omdat we wilden nagaan of de interactie tussen taal en perceptie echt niet in de visuele hersenschors plaatsvindt, lieten we de proefpersonen de woorden dit keer met volledige aandacht lezen, zodat de talige informatie actief werd verwerkt. Dit resulteerde in sterkere effecten: het verschil in reactietijden en in aantallen fouten tussen congruente en incongruente condities was veel groter dan in hoofdstuk 2, waar proefpersonen de woorden mochten negeren. Ondanks deze grotere effecten op gedragsniveau was nog steeds alleen de linker temporaalkwab betrokken bij het integreren van de talige en visuele informatie - en we vonden opnieuw geen effecten in visuele hersengebieden.

In hoofdstuk 5 wilden we bekijken of meer specifieke woorden een ander effect hebben op visuele waarneming dan meer algemene woorden. Als je het woord ölifant"leest, vormt zich dan een meer gedetailleerd beeld in je hoofd dan wanneer je het woord "dier"leest? We lieten proefpersonen eerst kort een woord lezen, bijvoorbeeld "hamerën toonden daarna een plaatje van een dier of een gereedschap (zie figuur 7.6). Op die manier creëerden we weer congruente condities - waarbij het woord klopte met het plaatje ("hamer"+ plaatje van hamer) en incongruente condities (ölifant"+ plaatje van hamer).

De specifieke woorden leidden ertoe dat proefpersonen congruente plaatjes sneller konden categoriseren dan incongruente plaatjes. Maar ook de woorden die een categorie beschreven, "dieröf "gereedschap", hadden tot effect dat de plaatjes sneller gecategoriseerd konden worden als het woord klopte met de categorie van het plaatje ("dier"+ plaatje van olifant). Uit onze fMRI-data bleek dat opnieuw de linker temporaalkwab



Figuur 7.6: Proefpersonen zagen een grijs computerscherm met daarop eerst een woord (bijvoorbeeld ölifant") en kort daarna een plaatje van een dier of een gereedschap (bijvoorbeeld een kreeft). Ze moesten vervolgens zo snel mogelijk kiezen of op het plaatje een dier of een greedschap te zien was.

betrokken was bij de integratie van de twee informatiebronnen. We vroegen ons vervolgens af of er in de hersenen een verschil zou zijn tussen het effect van specifieke versus algemene talige informatie op perceptie. Een congruente specifieke beschrijving, zoals ölifant"gevolgd door een plaatje van een olifant, resulteerde in minder activiteit in de vroege visuele cortex dan een incongruente specifieke beschrijving ("hamer"+ plaatje van olifant). Dit effect was er niet voor de woorden die aan een categorie refereerden. Echter, de fMRI resultaten in hoofdstuk 5 waren niet robuust genoeg om sterke conclusies te kunnen trekken.

Het verplaatsen van je aandacht naar bepaalde aspecten van een plaatje doet je soms een eend, en soms een haas zien. Onze studies tonen aan dat taal, net als aandacht, kan beïnvloeden hoe je iets waarneemt. Woorden kleuren ons wereldbeeld zelfs ongemerkt, als je niet eens weet dat je ze gelezen hebt. Blijkbaar zijn de associaties tussen woorden en de dingen die ze beschrijven zó sterk, dat alles wat we zien automatisch 'vertaald' wordt in een meer conceptuele vorm, waarna deze twee bronnen van informatie geïntegreerd worden in ons taalsysteem.

Dat taal een machtig middel is, hebben geschiedenis en politiek, kunst en literatuur, religie en commercie overtuigend bewezen. Uit de onderzoeken in dit proefschrift blijkt dat woorden zelfs een fundamenteel proces als onze waarneming kunnen veranderen. We dragen een soort onzichtbare bril waardoor we naar de wereld kijken: geen roze bril, maar een bril van taal.

LIST OF PUBLICATIONS

JOURNAL ARTICLES

1. Francken, J.C., van Gaal, S., and de Lange, F.P. (2011). Immediate and long-term priming effects are independent of prime awareness. *Consciousness and Cognition*, 20(4), 1793-1800.

2. Francken, J.C., van Gaal, S., and de Lange, F.P. (2012). Response to Desender and Van den Bussche: On the absence of a relationship between discriminability and priming.*Consciousness and Cognition*, 21(3), 1573-4.

3. Willems, R.M. and Francken, J.C. (2012). Embodied semantics: Taking the next step. *Frontiers in Psychology*, 3.

4. Francken, J.C. and Slors, M. (2014). From commonsense to science, and back: The use of cognitive concepts in neuroscience. *Consciousness and Cognition*, 29, 248-58.

5. Francken, J.C., Kok, P., Hagoort, P. and de Lange, F.P. (2015). The behavioral and neural effects of language on motion perception.*Journal of Cognitive Neuroscience*, 27(1), 175-84.

6. Francken, J.C., Meijs, E.L., Ridderinkhof, O.M, Hagoort, P., de Lange, F.P., van Gaal, S. (2015). Manipulating word awareness dissociates feed-forward from feedback models of language-perception interactions.*Neuroscience of Consciousness*, 1.

7. Simanova, I., Francken, J.C., de Lange, F.P., Bekkering, H. (2015). Linguistic priors shape categorical perception. *Language, Cognition and Neuroscience*, 1-7.

8. Francken, J.C., Meijs, E.L., Hagoort, P., van Gaal, S., de Lange, F.P. (2015). Exploring the automaticity of language-perception interactions: Effects of attention and awareness. *Scientific Reports*.

9. Francken, J.C. and Slors, M. (in preparation). Neuroscience and everyday life: Facing the translation problem.

OTHER PUBLICATIONS

1. Francken, J.C. (2012). Help, mijn hersenen getuigen tegen mij! *Actioma, Juridisch Faculteitsblad*, 183, 41-43.

2. Francken, J.C. (2013). Schrijven versus typen: wat zegt de neurowetenschap? *4W Kennisnet*, 3, 6-13.

DANKWOORD

Dit proefschrift voelt als de kroon op meer dan 28 jaar lang leren - mijn grootste hobby. Iedereen hieronder heeft daar aan bijgedragen.

Peter, ik herinner me onze eerste ontmoeting, in juli 2009, nog goed. We spraken elkaar omdat ik een debat over vrije wil organiseerde met happyChaos, en jij toen een van de weinige neurowetenschappers was die daarover had geschreven. Achteraf zag ik pas hoezeer deze ontmoeting jou kenmerkt. Het raakt aan je enorm brede interesse: van hersenen, taal, filosofie, tot politiek, literatuur, poëzie. Het illustreert het feit dat je ongekend goed kunt organiseren op allerlei niveaus: je onderzoeksgroep, het Donders en MPI, Spinozawinnaars, de wereldwijde Neurobiology of Language community. Het toont jou als pleitbezorger voor het vertalen van wetenschap naar de echte wereld. Waar heb je me niet mee naartoe genomen? De KNAW, de koningin, Paradiso, naar het Nobelprijswalhalla Lindau. Dankzij jou heb ik me de afgelopen vier jaar niet alleen ontwikkeld als zelfstandig hersenonderzoeker, maar bovenal als veelzijdig academicus. Je bent de meest inspirerende leermeester die ik me kan wensen.

Floris, dankzij jou ben ik gefascineerd geraakt door hersenen. Als onbeschreven blaadje mocht ik in 2010 een onderzoeksstage bij jou doen en vervolgens mijn promotieonderzoek. Alles wat ik nu weet en kan, heb jij me geleerd. En door je enthousiasme, geduld en kritische vragen heb je me vijf jaar lang uitgedaagd om beter na te denken. Maar niet alleen om die reden was onze samenwerking een groot feest. Je bent een toonbeeld van hoe werken in de wetenschap en een leuk leven leiden samen kunnen gaan. Daarom gingen onze gesprekken voor een belangrijk deel over Amsterdam, muziek en belevenissen buiten het Donders - en vonden plaats op een terrasje, feestje of tijdens een etentje. Het is fantastisch om jou als voorbeeld te hebben.

Simon, jij was er ook vanaf het begin bij. In goede en in slechte tijden heb je me vooruitgeholpen en aangemoedigd. In de loop der jaren zijn onze gezamenlijke activiteiten verschoven van werktijd - projecten opzetten en papertjes schrijven - naar vrije tijd - borrels, feestconferenties en chillen in je grachtenpand. Hopelijk kunnen we deze succesformule in de toekomst voortzetten op de UvA. Je laat me zien dat wetenschap ook relaxt en gezellig kan zijn.

Peter, zonder jou had ik geen enkele analyse tot een goed einde kunnen brengen. Met engelengeduld heb je me vrienden leren worden met MATLAB. Je had steevast tijd om me te helpen, wat vaker wel dan niet nodig was. Als ouwe rotten in de predatt groep organiseerden we de eerste retreat en later jouw symposium.

Roel, bij jou kon ik altijd terecht voor rust en relativering. Ik bewonder de zelfverzekerde manier waarop je onderzoek doet en je eigen richting kiest.

Marc, jouw enthousiasme is ongeëvenaard. Ik ben nog altijd blij dat ik je heb uitgenodigd voor mijn BBM lezing over common sense concepts - daar is het allemaal mee begonnen. Het schrijven van ons artikel was als een avontuur waarvan ik de afloop niet precies wist. Door onze gesprekken - en niet te vergeten, discussies - heb je me geholpen

om telkens afstand te nemen van mijn specialistische vakgebied en er filosofische vragen bij te stellen. Ik verheug me erop met je te blijven werken en samen de manier waarop neurowetenschappers denken en werken een klein beetje te veranderen.

Erik, wat was het een voorrecht om jou als masterstudent te begeleiden. Hoewel van begeleiden nauwelijks sprake was - ik zou het samenwerken willen noemen. Zomerweekenden in de kelder bij de scanner en uren puzzelend op weerbarstige scriptjes, waarmee jij iedere dag weer met veel enthousiasme aan de slag ging. Ik heb van jou minstens zoveel geleerd als jij van mij.

Eric, ik ken weinig wetenschappers die zo van onderwijs houden als jij. Je hebt mij alle ruimte gegeven om mijn ideeën in de praktijk te brengen en moedigde me aan om me te ontwikkelen als docent.

Jeanette en Sander, wie anders zouden mijn paranimfen moeten zijn?! Samen zijn we begonnen aan het PhD avontuur en samen hebben we alle stadia doorlopen. Eeuwig wachten op het eerste paper, karaokebars onveilig maken, de balans vinden tussen onderzoek en alles eromheen, urenlange gesprekken over onze toekomstplannen. Jeanette, het was ongelooflijk fijn dat ik altijd je parttime huisgenoot mocht zijn. Sander, ik heb genoten van je onwankelbare optimisme - in de trein of als buren in kamer 1.18 en 1.20.

Tim, treinreizen werd een feestje dankzij jou. Zoveel uren per dag om alles te delen - van muziek en films tot ontbijtjes en filosofische literatuur.

predatters, what an inspiring group of people you are. Guided by our common hero Floris, we grew from Peter, Ana, Sasha, Freek, Shanti, Marius into a big group with Simon, Anke Marit, Loek, Matthias, Claudia, Elexa, Eelke, Pim, Erik, Christian, Erik, Remco, Lieke, Matthias and some shorter or longer stopovers by Matthew, LiYan, Doby, Lies, Michel, Yvonne, Andrea, Bronagh, Simone, Aureliane, Nathalie, Vanessa, Larisa, Poppy, Thomas, Heidi, Mariya and Felix. While bigger now, the predatt atmosphere is still unmatched: open, happy, collaborative and critical but constructive.

The Neurobiology of Language group is a professional yet sociable place to be. I enjoyed our lab meetings and PhD meetings Peter, Roel, Dan, Karl-Magnus, Marcel, Hartmut, Jan-Mathijs, Julia, Kirsten, Tineke, Monique, Diana, Chu, Kirsten, Alex, Lennart, Vicky, Hubert, Geertje, Anne, Annika, Katrien, Laura, Lin, Miriam, Huadong, Zheng, David, Jana, Alina, Izabela, Flora, Ashley, Franziska, Nietzsche, Evelien, Richard, Gwilym, Matthias, Bohan, Daniel, Salomi, Irina, Annabel, Lotte, Dalya, Danchao, Jolien, Louise, Johanne, Sarah (and everyone I forget!). Laura, Lotte and Evelien, I am proud that together we managed to make hettaligebrein.nl and our MPI group website such a success. Being part of the Neurobiology of Language group, I was fortunate to meet several MPI'ers during the retreat, and prediction and webcom meetings: Mark, Ina, Ad, Will, Joost, Antje, Stephen, and Simon, to name a few.

Noortje, Matthias, Daphne, Dirk, Bart, Stephanie, Diana, and Zahra, it was a great pleasure to have you as my roommates. The outside world only gets to see the end products, but we know how much hard work this requires every day. Peter, you made me feel welcome back in the days in student room 0.98.

I had the opportunity to supervise various students for shorter or longer periods. Thank you Odile, Claudia, Annabel, Angela, Lies, Alessandra, Erik, Nadine, Anne, Caitlin, Heidi and Toru for your enthusiastic contribution to and interest in my research projects.

Working at the Donders is fun because of the omnipresence of Social Donderians.

Without being exhaustive, over the past years they compromised Eelke, Sander, Jeanette, Anke Marit, Loek, Mirjam, Tim, Jeroen, Sasha, Mirre, Winke, Susanne, Richard, Joost, Hanneke, Lieneke, Monja, Mao, Lisa, Linda, Vincent, Madelon, Rene, Linda, Ruud, Dirk, Rick, Lennart, Miriam, Anke, Atsuko, Stephen, Matthias, Tom, Mariet, Alex, Flora, Ruben, Eelco, Verena, Tobias, Joachim, Ruth, Corina, Marcel, Niccolo, Stan, Rasim, Marlieke, Sean, Arjen, Til, and at the DCC Frank, Roemer, Sybrine, Mark, Egbert, Irina. I enjoyed your company and all of our shared experiences, such as the Dagje Uit, Thursday lunches, karaoke nights, conferences, drinks and easter egg hunts.

Working at the Donders is also wonderful because there is so much to learn from our group of extremely talented and inspiring PI's, among which Peter, David, Floris, Ivan, Roshan, Alan, Guillén, Christian, Christian, Janneke, Ole, Karin, Marcel, and Harold. All of us would not have produced any paper without the superior support of the technical group - Paul, Erik, Marek, Edward, Rene, Uriel, Mike, Jessica, Hong, and Sander – and the good care of the administration team - Tildie, Arthur, Sandra, Nicole, Ayse, Joost, Petra.

During my PhD, there were many opportunities to develop myself as an academic. I very much liked organizing the Foundations Meetings together with Eelke, during which we discussed a wide array of topics from a philosophical perspective. Also outside of the Trigon I enjoyed participating in many discussion groups, at the DCC with Pim, Iris, Mark, and others, at the Philosophy department with Marc, Leon, Derek, Fleur and Katja, and at the KNAW with a group of Daniel Dennett fans (and the master himself). In addition, I got the opportunity to practice my science communication skills during the fantastic open day in the Brain Awareness Week, organized together with Jeanette, Arthur, Cerien, Sabine, Andrei, Saskia, Marten, and Richard, and in several encounters with Radboud science communication team Iris and Iris.

Op de terugweg, in de trein van Nijmegen naar Amsterdam, wist ik dat er altijd een schare UvA'ers was waar ik op kon bouwen tijdens conferenties – en dan met name NVP - waaronder Anouk, Simon, Martijn, Anne en Iris.

En daar, in Amsterdam, was het tijd voor mijn liefste vrienden Emma, Wouter, Naomi, Femke, Mascha, Bas, Maurits. Ondanks dat ik de afgelopen jaren vaak niet wist waar ik de tijd vandaan moest halen om jullie te zien, waren jullie er altijd voor mij. Om te kletsen, thee te drinken, naar festivals of Paradiso te gaan, voor pizza-avonden en nog veel meer. Ook was het heerlijk om op woensdagavond of in Hattem de wereldproblematiek door te spreken met wat Chaoten.

Voor mijn Donderstijd is al een belangrijke basis voor dit proefschrift gelegd. Pieter heeft me opgeleid tot kritische en enthousiaste filosoof. Yvo heeft me de beginselen van het wetenschappelijk onderzoek geleerd. Op het Stedelijk Gymnasium Haarlem en op de Haarlemse Montessorischool kreeg ik de vrijheid om mijn honger naar kennis te stillen.

Al die jaren ben ik aangemoedigd en bijgestaan door mijn lieve (schoon)familie. Mijn oma's, Anneke en hooggeleerde opa's, altijd geïnteresseerd in wat me bezighoudt, altijd trots. Rud, Marjolein, Sander, wat voel ik me thuis bij jullie. Lieve Yara, wat is het fijn om jou als zus te hebben, en wat blijft het leuk dat ik Klaas en Wietske en Martijn ook tot mijn broers en zussen mag rekenen. Hajo en Liesbeth, pappa en mamma, dankzij jullie ben ik geworden wie ik ben. Jullie hebben me de afgelopen 29 jaar onafgebroken omringd met oneindig veel liefde. Iedere dag leven jullie met me mee. Liefste Peter, wat bijzonder om samen doctor te worden. Het leven met jou is het mooiste feest dat er bestaat.

CURRICULUM VITAE

Jolien C. FRANCKEN

Jolien Francken was born in Groningen on October 11, 1986. She graduated from high school at the Stedelijk Gymnasium Haarlem in 2004. She completed a MA in Philosophy (2010, cum laude) as well as a MSc in Medicine (2011, cum laude) including minor programs in Practical Philosophy and Dutch Literature History at the University of Amsterdam. From 2009, she organized debates and symposia for students on societal, cultural and political issues with happyChaos. During the course of her studies, she completed a research internship at the Neurology department of the Academic Medical Centre in Amsterdam with prof. dr. Yvo Roos about the effects of the implementation of a stroke unit on the recovery of stroke patients. In a second research internship at the Donders Institute for Brain, Cognition and Behavior in Nijmegen with dr. Floris de Lange she studied inter-individual differences in structure and function of neural networks involved in multisensory integration.

In May 2011 she started a PhD at the Donders Institute under supervision of prof. dr. Peter Hagoort and dr. Floris de Lange. Her PhD research focused on the neurobiological and psychological mechanisms of the effect of language on visual perception. During her PhD, she participated in the 64th Lindau Nobel Laureate Meeting, a conference with 40 Nobel Prize winners and 600 young scientists, and she co-founded the Theoretical and Philosophical Foundations of Neuroscience meetings at the Donders Institute. Enjoying science communication, she co-organized a successful open day with workshops, seminars and debates to interactively share neuroscience research with the general public at the Donders Institute during the Brain Awareness Week in 2012 and she initiated and edited *hettaligebrein.nl*, a weekly blog featuring research on language and the brain. She obtained her basic teaching qualification certificate in 2014.

Jolien Francken is currently a lecturer at the Institute for Interdisciplinary Studies and the Psychology Department of the University of Amsterdam. Besides, she is writing a popular science book on the role of language in visual perception, to share her scientific work with a general audience.

DONDERS SERIES

1. Van Aalderen-Smeets, S.I. (2007). *Neural dynamics of visual selection.* Maastricht University, Maastricht, the Netherlands.
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